

### 5.1 Introduction

Although this chapter is entitled 'Predation', we shall be dealing in it with a variety of interactions. In all the cases we shall be considering, however, animals will totally consume, or partly consume and also harm, other animals or plants. This broad umbrella is designed to include each of the following categories of 'predator'.

1 *True predators* that consume other animals—their *prey*—and thus gain sustenance for their own survival and reproduction.

2 *Parasitoids*. These are insects, mainly from the order Hymenoptera, but also including many Diptera, which are free-living in their adult stage, but lay their eggs in, on or near other insects (or, more rarely, spiders or woodlice). The larval parasitoids then develop on or within their '*host*' (usually, itself, a pre-adult), initially doing little harm, but eventually almost totally consuming, and therefore killing, the host prior to pupation. Often just one parasitoid develops from each host, but in some species several individuals share a host. Nevertheless, in either case, the number of hosts attacked in one generation closely defines the number of parasitoids produced in the next. This, along with the fact that the act of 'predation' is confined to a particular phase of the life history (adult females attacking hosts), means that parasitoids are especially suitable for study. They have provided a wealth of information relevant to predation generally.

3 *Parasites*. These are organisms (animals or plants) that live in an obligatory, close association, usually with a single *host* individual for a large portion of their lives. They gain sustenance from their host and do their host harm, but parasite-induced host mortality is by no means the general rule, and is often rather rare.

4 *Herbivores*. These are animals that eat plants. Some appear to act as true predators, since they totally consume other organisms for their own sustenance (seed-eaters are a particularly good example). Others

are much more like parasites; aphids, for instance, live in close association with plant hosts, gain sustenance from them, and reduce their vitality. Many other herbivores, however, fall into neither category. They do not live in close association with any one plant host; but by consuming parts of plants, they are often the ultimate, if not the immediate, cause of plant mortality. Thus, they certainly do have a detrimental effect on their plant '*prey*'.

These four categories are all quite distinct and special in their own way, but, as their inclusion within a single definition shows, they share important common features. For this reason there will be many statements in this chapter that apply to all categories. It would be tedious to refer individually in every such case to 'true predators and their prey, parasitoids and their hosts, parasites and their hosts, and herbivores and their food plants'. Instead, for simplicity, and where the context precludes ambiguity, the four categories will be referred to, together, as predators (or, rarely, consumers) and their prey.

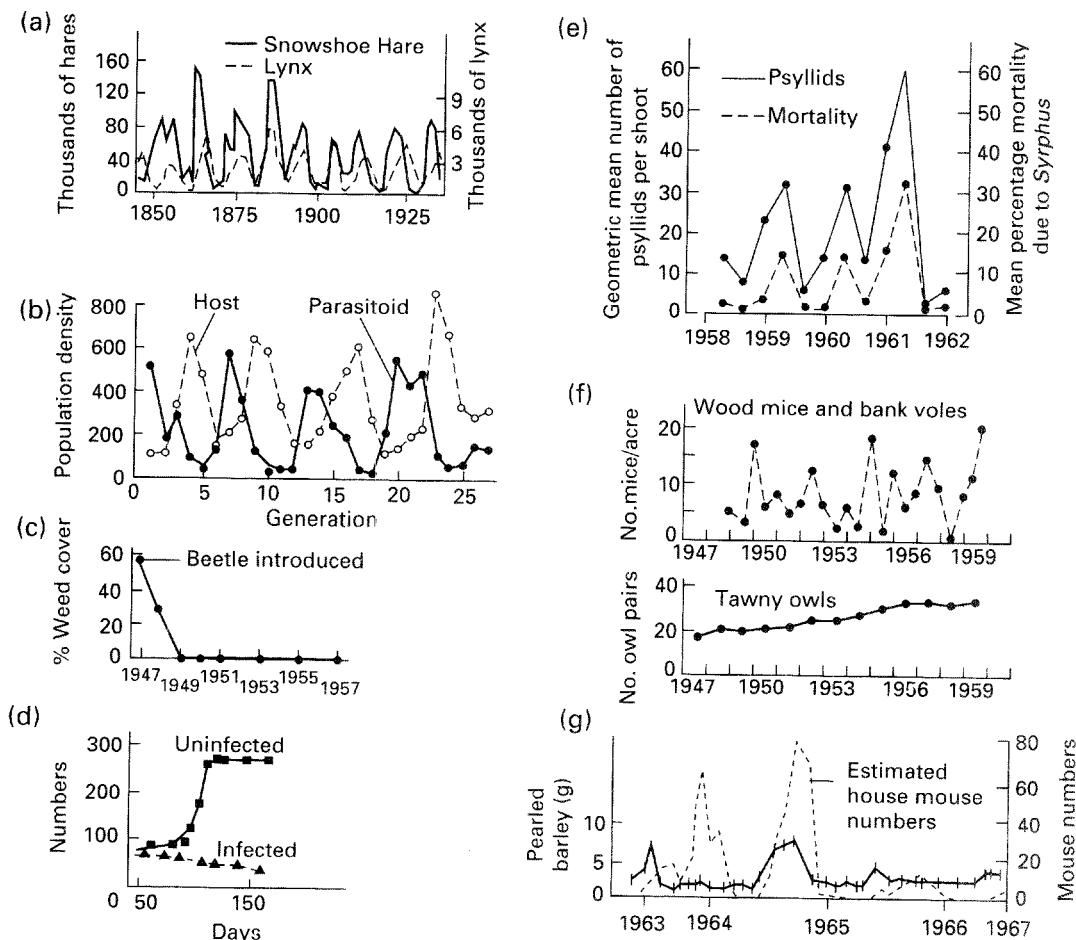
We can, therefore, apply a single definition and a single, all-embracing label to these four categories. But we can also apply a single naive expectation regarding their population dynamics. If we imagine a *single* species of predator and a *single* species of prey, then we can expect predators to increase in abundance when there are large numbers of prey. However, there should then be an increase in predation-pressure on the prey, leading to a decrease in prey abundance. This will ultimately lead to food-shortage for the predators, a decrease in predator abundance, a concomitant drop in predation-pressure, an increase in prey abundance and so on. In other words, there appears, superficially, to be an inherent tendency for predators and their prey (and parasitoids and their hosts, parasites and their hosts, and herbivores and their food plants) to undergo *coupled oscillations* in abundance, predator numbers 'tracking' those of the prey.

## 5.2 Patterns of abundance

Some actual examples of abundance patterns are shown in Fig. 5.1. Certainly, some do appear to show coupled oscillations (Fig. 5.1a & 5.1b), but there are also cases in which the 'prey' are kept at a constant low level (Fig. 5.1c & 5.1d), cases in which the prey

exhibit periodic outbreaks (Fig. 5.1e), and cases in which the 'predators' have no noticeable, simple effect on the prey since the fluctuations in the sizes of the two populations are apparently unconnected (Fig. 5.1f & 5.1g).

It is clear, in other words, even from this limited range of examples, that *actual* predators, parasitoids,



**Fig. 5.1** Patterns of abundance in predator-prey systems. (a) The lynx *Lynx canadensis* and the snowshoe hare *Lepus americanus*; true predator-prey. (After MacLulich, 1937.) (b) The wasp *Heterospilus prosopidis* and the bean weevil *Callosobruchus chinensis*; parasitoid-host. (After Utida, 1957.) (c) Changes in the abundance of the Klamath weed *Hypericum perforatum* following the introduction of the leaf-eating beetle *Chrysolina quadrigemina*; herbivore-plant. (After Huffaker & Kennett, 1959.) (d) The effect on the

beetle *Laemophloeus minutus* of being infected by the protozoan *Mattesia dispersa*; parasite-host. (After Finlayson, 1949.) (e) The psyllid *Cardiaspina albitextura* and mortality caused by *Syrphus* species; true predator-prey. (After Clark, 1963.) (f) Tawny owls *Strix aluco* and wood mice and bank voles *Apodemus sylvaticus* and *Clethrionomys glareolus*; true predator-prey. (After Southern, 1970.) (g) The house mouse *Mus musculus* and barley *Hordeum vulgare*; herbivore-plant. (After Newsome, 1969a.)

parasites, herbivores and their 'prey' all exhibit a wide variety of patterns of abundance, and we can immediately see two rather obvious reasons for this. The first is that predators and prey do not normally exist as simple, two-species systems. To understand the abundance patterns exhibited by two interacting species, these must be viewed in a realistic, multi-species context. The second reason is that our conception of even the simplest, abstracted, two-species system is itself excessively naive. Before multi-species systems are even considered, we must abandon our expectation of universal prey-predator oscillations, and look instead, much more closely, at the ways in which predators and their prey interact in practice.

We shall examine, in turn, the individual components of the predator-prey relationship (an approach employed successfully by Hassell, 1976, 1978); but the journey covering these components will be a long and fairly complicated one. Moreover, it is only *after* all the topics have been examined in detail that we shall be able to reassemble them into an integrated whole. At this stage, therefore, we provide an itinerary which can be referred to now or part-way through the journey. This is set out in Table 5.1, and in the following outline of the rest of this chapter.

In section 5.3, the patterns of food preference shown by predators are examined, along with some possible determinants of these patterns. Then, in section 5.4, a number of effects of time scales and timing are considered. This is followed by an examination of the detailed effects of predators on the fitness

of prey, paying special attention to the effects of herbivores on plants (section 5.5). Then, in section 5.6, consideration is given to the ways in which prey 'thresholds' and food quality complicate the relationship between predation-rate and the beneficial effects to the predator. Section 5.7 covers the way in which predation-rate is influenced by the availability (especially the density) of prey items; while a long section 5.8 considers some of the consequences of environmental heterogeneity (particular attention being paid to the unequal way in which many predators distribute their harmful effects amongst individual prey). In section 5.9, the consequences of mutual interference amongst predators are examined, and in section 5.10, the similarities between the effects produced by the processes in sections 5.8 and 5.9 are discussed. Then, in section 5.11 attention is drawn to the tendency of predators to maximize their 'profits' by 'foraging optimally'; while section 5.12 is a resumé of the preceding nine sections.

Throughout these sections we will be especially concerned with the effects that these individual components have on the dynamics of the predator and prey populations; and in particular, with the regulatory, stabilizing effects of density-dependent processes, and the destabilizing effects of inversely density-dependent processes (sections 2.3 and 2.6). Then, in section 5.13, we attempt to incorporate many of the behaviourally complex components into models of predator-prey interactions, hoping to explore further their effects on population dynamics and stability; and this allows us, in section 5.14, to reconsider the abundance patterns of the present section in the light of sections 5.3–5.13. Finally, section 5.15 examines problems emanating from the contrived human predation involved in the process of harvesting.

Table 5.1 Summary of the components of the predator-prey interaction which are examined in this chapter.

Effect of	On	Section
evolution	predator specialization	5.3
time scales	patterns of abundance	5.4
prey density	prey	5.5
predation-rate	prey	5.5
predation-rate	predator	5.6
prey density	predation-rate	5.7
aggregation	predation-rate	5.8
mutual predator interference	predation-rate	5.9
foraging strategies	predation-rate	5.11

### 5.3 Coevolution, and specialization amongst predators

Predators of all types can be classified, according to their diet width, as monophagous (feeding on a single prey type), oligophagous (few prey types) or polyphagous (many prey types), and the degree of specialization can have important effects on predator-prey dynamics.

The abundance of a monophagous predator, for instance, is likely to be closely linked to the distribution and abundance of its prey; while a polyphage is very unlikely to have its abundance determined by any one of its prey types. If we are to understand the patterns of diet width amongst predators, however, we must begin by establishing two basic points. The first is that *predators choose profitable prey*. This follows, by an act of faith, from a consideration of natural selection (evolution favours those individuals with the highest

fitness; fitness is increased by increasing the profitability of food-acquisition; evolution, therefore, favours predators that choose profitable prey). It is also borne out by the facts. Figure 5.2, for instance, illustrates examples of predators actively selecting those prey items which are most profitable, i.e. prey items for which the gain (in terms of energy intake per unit time spent handling prey) is greatest.

The second point stems from the fact that all animals and plants have evolved in response to selection pressures originating, to a large extent, from the other animals and plants in their environment. The point, then, is that *predators and their prey are likely to have coevolved*. There is a continuous selection pressure on prey to avoid death (or, more generally, fitness-reduction) at the hands of their predators, and a reciprocal, continuous pressure on predators to increase *their* fitness by exploiting their prey more effectively. At perhaps its most trivial, this evolutionary arms race consists of prey that can run quickly from their predators, and predators that can run quickly after their prey, both being favoured by natural selection. However, we can see the results of analogous pressures on prey in the distasteful or poisonous chemicals in the leaves of many plants, in the spines of hedgehogs, the camouflage coloration of many insects, and the immunological responses of hosts to parasite infection; while in predators these pressures results, for instance, in the long, stout, penetrative ovipositors of wood wasps, the hooks and suckers on the heads of tapeworms, and the silent approach and sensory excellence of owls. It is clear, in short, that no natural predator-prey interaction can be properly understood unless it is realized that each protagonist has played an essential role in the evolution of the other.

It is equally clear, however, irrespective of any coevolution, that no predator can possibly be capable of consuming all types of prey; simple design constraints prevent shrews from eating owls, and humming-birds from eating seeds. Nevertheless, coevolution provides an added force in the restriction of diet width. Each prey species responds (in an evolutionary sense and on an evolutionary time scale) in a different way to the pressures imposed by its predators,

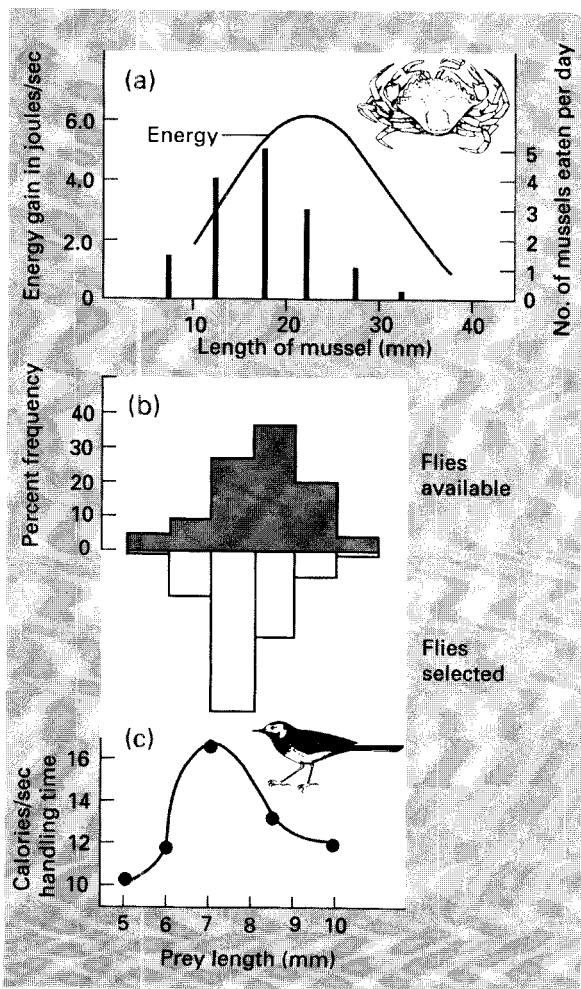


Fig. 5.2 Predators eating 'profitable' prey: (a) crabs eating mussels (Elner & Hughes, 1978); (b) pied wagtails eating flies (Davies, 1977). (After Krebs, 1978.) 1 calorie (non-SI unit) = 4.186 joules.



but a predator cannot 'coevolve' in a wide range of directions simultaneously. Predators, therefore, tend to specialize to a greater or lesser extent, and the better adapted a predator is for the exploitation of a particular prey species, the less likely it is to profit from the exploitation of a wide variety of prey. Parasites, in particular, because they live in such intimate association with their hosts, tend to specialize, evolutionarily, on a single host species. Their whole life style and life cycle is finely tuned to that of their host, and this precludes their being finely tuned to any other host species. They are, therefore, commonly monophagous. For similar reasons, the same is true of many parasitoids, although in their case, possibly because they are free-living as adults, polyphagy (or at least oligophagy) is rather more common.

Conversely, with herbivores and predators the situation is much less clear-cut. At one extreme there are examples of complete monophagy. The fruit fly, *Drosophila pachea*, for example, indigenous to the Sonoran Desert of the south-west USA, is the only species capable of consuming the rotten tissues of the Senita cactus (and its associated micro-organisms), because all other species are poisoned by an alkaloid—pilocereine—which the Senita produces (Heed *et al.*, 1976). Moreover, natural selection has favoured *D. pachea*'s exploitation of this exclusive niche to such an extent that the fly has an absolute requirement for certain unusual sterols which are also only produced by the Senita. Many plants produce 'secondary', protective chemicals and, probably as a consequence, many herbivorous insects are specialists (Lawton & McNeill, 1979; Price, 1980). However, most true predators and many herbivores feed on a variety of prey items.

A partial explanation of the range of diet widths is provided by a simple consideration of the fact that, although there is pressure from coevolution towards predator specialization, there is a counterbalancing evolutionary pressure discouraging the reliance of predators on an unpredictable or heavily exploited resource. For many parasites, the necessity for specialization clearly provides a pressure that outweighs any disadvantages stemming from resource unpredictability; for *D. pachea*, specialization is presumably fa-

voured by the exclusivity (and, perhaps, predictability) of the Senita, and the consequent lack of interspecific competition. To a certain extent, similar arguments can be advanced to explain diet width generally. Thus, where prey exert pressures which demand specialized morphological adaptation by the predator, there is a tendency for the predator to have a narrow range of diet; and where predators feed on an unpredictable resource, there is a tendency for them not to be specialists.

### 5.3.1 One explanation for the degrees of specialization

In many cases, however, some further explanation is needed, and this may be provided by the ideas of MacArthur and Pianka (1966; see also MacArthur 1972). In order to obtain food, any predator must expend time and energy, first in *searching* for its prey, and then in *handling* it (i.e. pursuing, subduing and consuming it). Searching will tend to be directed, to some degree, towards particular prey types; but, while searching, a predator is nevertheless likely to encounter a wide variety of food items. MacArthur and Pianka, therefore, saw diet width as being determined by the choices made by predators once they had encountered prey. Generalist predators are those that choose to pursue (and, hopefully, subdue and consume) a large proportion of the prey they encounter; specialists are those that continue searching except when they encounter prey of their specifically preferred type.

The basic conclusion MacArthur and Pianka drew from these considerations can be stated as follows. Predator choices are determined, ultimately, by the forces of natural selection, and are driven by these forces towards the maximization of profitability for the predator. Natural selection, therefore, favours a predator that chooses to pursue a particular prey item *if*, during the time it takes to handle *that* prey item, the predator cannot expect to search for *and* handle a more profitable prey item. On this basis, predators with handling times that are generally short compared to their search times should be catholic in their tastes, because in the short time it takes them to handle a

prey item which has already been found, they can barely begin to search for another prey item. This is MacArthur and Pianka's explanation for the broad diets of many insectivorous birds that 'glean' foliage. Search is always moderately time-consuming; but handling the minute, stationary insects takes negligible time and is almost always successful. Ignoring such prey items (i.e. narrowing diet width) would, therefore, decrease overall profitability, and the birds tend to be generalists.

By contrast, many other predators have search times that are short relative to their handling times. In such cases, specialization will be favoured, because the predators can expect to find a more profitable food item very soon after ignoring a less profitable one. Lions, for instance live more or less constantly in sight of their prey so that search time is negligible; conversely, handling time and particularly pursuit time, can be very long (and energy-consuming). Lions consequently *specialize* on those prey that can be pursued most profitably: the immature, the lame and the old. Thus, on the basis of MacArthur and Pianka's ideas we can expect pursuers or handlers (like lions) to have relatively narrow diets, and searchers to have relatively broad ones. Along similar lines, Recher (in MacArthur, 1972) found that great blue herons in the *productive* waters of Florida (in which search times were consequently short) had a much narrower range of food size in their diet than those inhabiting the *unproductive* lakes of the Adirondacks (where search times were relatively long).

Clearly, we can go some way at least towards an understanding of the degrees of specialization shown by predators.

### 5.3.2 Food preference and predator switching

Irrespective of this range of diet width, however, polyphagy is very common; especially amongst predators and herbivores. Yet polyphagous animals are rarely indiscriminate in the various types of food they eat. Horton (1964), for example, presents the results of an accidental field experiment in which deer broke into a plantation containing four species of tree arranged at random; white pine, red pine, jack pine

and white spruce. As Table 5.2 shows, the deer, with free and equal access to all four species, exhibited a fairly consistent preference for jack pine followed by white pine, with red pine being only lightly browsed and white spruce ignored. Such preference amongst polyphagous animals is, in fact, the general rule; but as Murdoch and Oaten (1975) have shown, there are two distinct forms that this preference can take.

An example of the simpler and much commoner form is shown in Fig. 5.3 (Murdoch, 1969). Two types of predatory shore snails, *Thais* and *Acanthina*, were presented with two species of mussel (*Mytilus edulis* and *M. californianus*) as prey, at a range of prey proportions. When the proportions were equal, the snails showed a marked preference for the thinner-shelled *M. edulis*. The line in Fig. 5.3 has been drawn on the assumption that they retained this same preference at other (unequal) proportions, and this assumption is clearly justified: irrespective of availability, the snails showed the same marked preference for the less protected prey, which they could exploit most effectively.

This can be contrasted with data of a rarer sort in Fig. 5.4a, obtained from an experiment in which the predatory water bug, *Notonecta glauca*, was presented

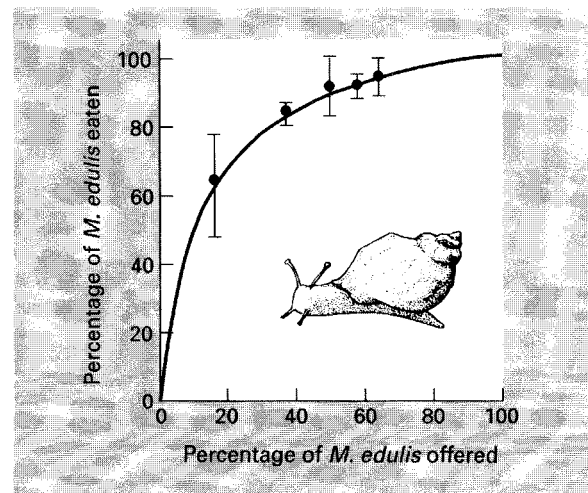


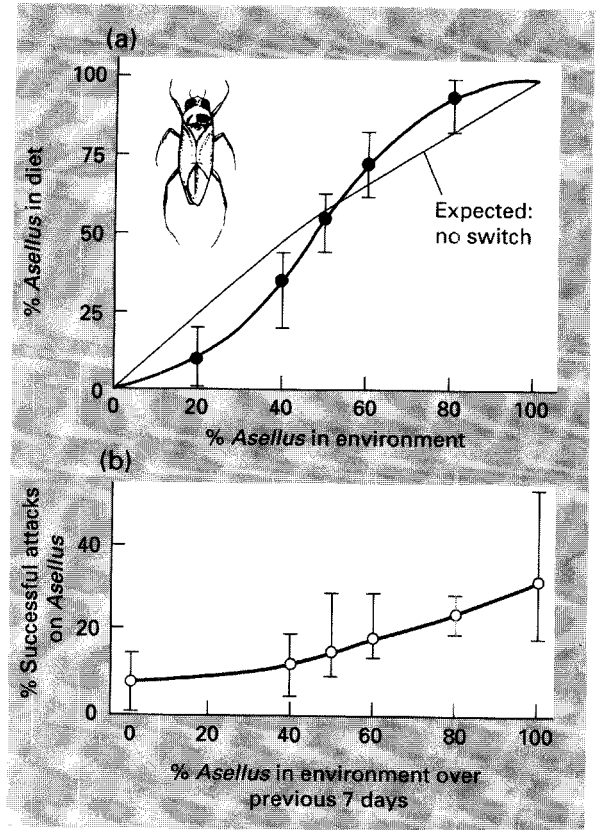
Fig. 5.3 Snails exhibiting a consistent preference amongst the mussels *Mytilus edulis* and *M. californianus* irrespective of their relative abundance (means  $\pm$  2 SE). (After Murdoch & Oaten, 1975).

**Table 5.2** Food preferences exhibited by deer. Percentage browsing incidence of deer on planted trees. (After Horton, 1964.)

	White pine	Red pine	Jack pine	White spruce
Winter 1956–57	31	19	84	0
Winter 1958–59	9	1	48	0
Winter 1960–61	17	0	70	0

with two types of prey—the isopod, *Asellus aquaticus* and mayfly larvae (*Cloeon dipterum*)—with overall prey density held constant (Lawton *et al.*, 1974). In this case the preference exhibited when the two prey types were equally available, if extrapolated to other availabilities (thin line in Fig. 5.4a), is obviously not a good indication of the overall response. Instead, *Notonecta* took a disproportionately small number of *Asellus* when they were scarce, and a disproportionately high number when they were common. This is known as *predator switching*, since it suggests that predators switch their preference to whichever prey is most common. In the case of *Notonecta*, the explanation is apparently illustrated in Fig. 5.4b: the more previous experience *Notonecta* has of *Asellus*, the more likely it is to make a successful attack. It appears, in other words, as if predator switching is based upon a learnt ability to specialize. This, essentially, is the view taken by Tinbergen (1960), who proposed that certain predators, particularly vertebrates, develop a 'specific searching image'. This enables them to search more successfully (since they effectively 'know what they are looking for'), and results in them concentrating on their 'image' prey to the relative exclusion of their non-image prey. Moreover, since the searching image develops as a result of previous experience, and since the predators (or herbivores) are most likely to experience common prey, we can expect predators to concentrate on a prey type when that type is common and switch to another prey type when it is rare.

The basis for predator switching has been discussed in more detail by Murdoch and Oaten (1975). One of their most instructive examples is the work of Murdoch, Avery and Smyth (in Murdoch & Oaten, 1975) on guppies offered a choice between fruit flies and



**Fig. 5.4** (a) The percentage of *Asellus* in the diet of *Notonecta* as a function of their relative abundance; the thinner line indicates the function expected on the basis of a consistent preference. (b) The effect of 'experience' on the success of *Notonecta* in attacking *Asellus*. (After Lawton *et al.*, 1974.) (Means and total ranges are indicated.)

tubificid worms as prey (Fig. 5.5). Figure 5.5a shows that there was, indeed, switching by the guppies. But more interesting than this is Fig. 5.5b, which shows that although the *population* of predators showed little preference when offered equal proportions of the two prey, the *individual* guppies showed considerable specialization. This does not contradict the idea of a search image, but does suggest that predator switching in a population does not result from individual predators gradually changing their preference, but from the *proportion of specialists changing*. Murdoch and Oaten provide evidence for the occurrence of this type of switching in other vertebrate predators, in some

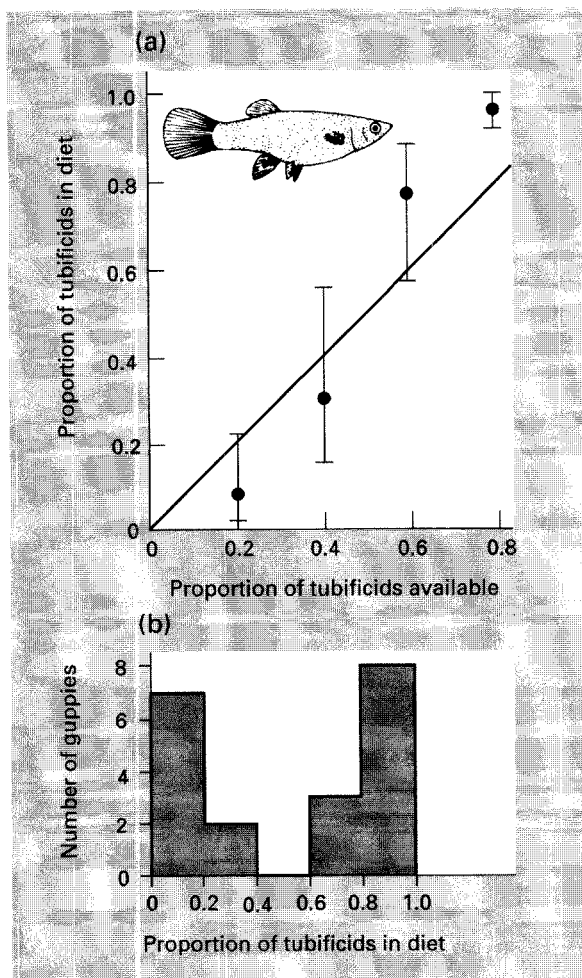


Fig. 5.5 (a) Switching in guppies fed on *Drosophila* and tubificids (with total ranges indicated). (b) A frequency histogram showing the number of individual guppies with particular types of diet when offered equal numbers of the two prey types. All showed a preference ( $< 0.4$  or  $> 0.6$ ) even though the population as a whole consumed approximately equal amounts of the two types. (After Murdoch & Oaten, 1975.)

invertebrate predators, and in a herbivore: the feral pigeon feeding on peas and beans (Murton, 1971). Nevertheless, it is fair to conclude that this more complex type of food preference is most common in vertebrates, where the ability to learn from experience is most highly developed. The consequences of it are discussed in section 5.7.4.

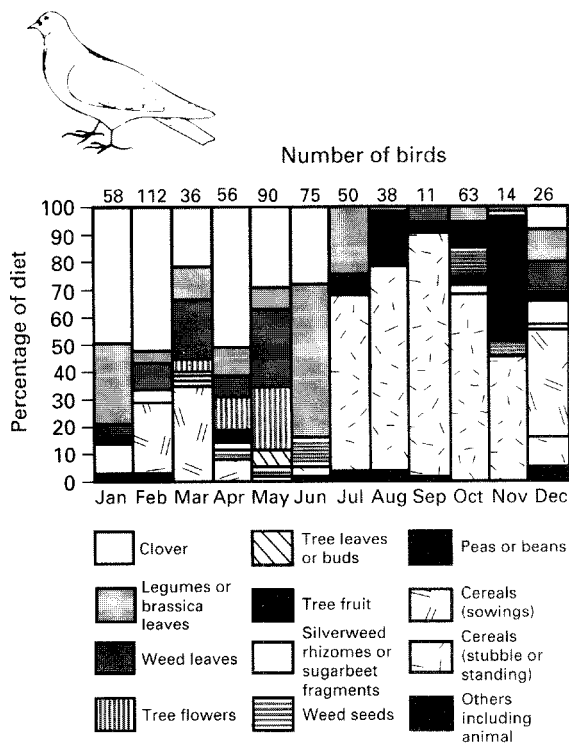


Fig. 5.6 Seasonal changes in diet. The percentage contributions of different food types to the diet of the wood pigeon *Columba palumbus* in Cambridgeshire, UK. (After Murton *et al.*, 1964.)

## 5.4 Time and timing

In any discussion of predation there are several points that must be made regarding the effects of time and timing. The first is that levels of specialization need not involve morphological adaptation, but may, in many cases, be the result of differing degrees of 'temporal' coincidence. Thus, the European rabbit flea (*Spilopsyllus cuniculi*), like very many parasites, has a life cycle that coincides more or less exactly with that of its host: maturation of the flea can only occur on a doe in the latter part of pregnancy, and eggs are laid only on the newborn rabbit young (Mead-Briggs & Rudge, 1960). The wood pigeon (*Columba palumbus*), by contrast, switches its food preference seasonally, depending on availability (Fig. 5.6; Murton *et al.*, 1964). Thus, while it may, at any one time, be fairly specialized in its feeding habits, it is temporally (as well as morpho-

gically) a generalist; and, unlike the parasite, its population dynamics are not strongly dependent on the availability of any one type of prey.

Related to the effects of temporal coincidence are the effects of differing lengths of life cycle amongst predators and their prey. Aphids, for instance, generally pass through several generations for each time their host plant passes through a seasonal cycle (never mind a generation). They can, therefore, be expected to react quickly towards, and fairly accurately reflect, the quantity and quality of their food. Conversely, the dynamics of a sycamore population is unlikely to be greatly influenced by the intraseasonal fluctuations in the abundance of its aphids. Similarly, small mammals, with a fairly high intrinsic rate of increase and a life span never exceeding a year, exhibit a pattern of abundance that reflects the yearly changes in environmental quality; while tawny owls in the same habitat, often living 6 years and failing to breed when food is scarce, maintain a comparative constancy of abundance irrespective of these environmental fluctuations (Southern, 1970).

In part such 'discrepancies' are the result of making comparisons on an artificial, yearly basis, when it might be more appropriate to consider the fluctuations from generation to generation. Nevertheless, it is quite clear that generation times, and in particular the relative generation times of a 'predator' and its 'prey', can have important effects on predator-prey dynamics through their influence on the speeds at which species respond to changes in the environment.

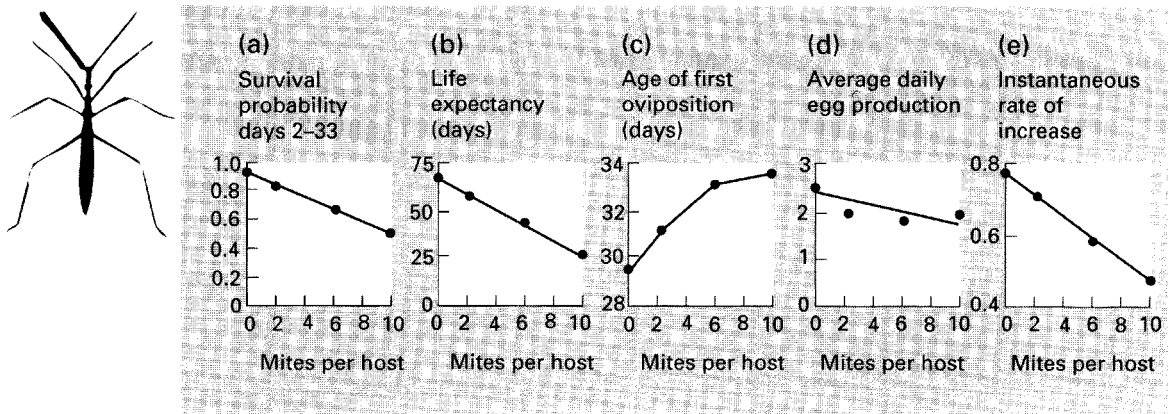
Another aspect of timing relevant to predator-prey dynamics is the effect of time-lags. We have already seen (in section 3.4.1) that time-lags tend to cause increased levels of fluctuation in dynamic systems (i.e. they tend to *destabilize* systems), and we can expect this to apply to populations of predators and their prey. Once again, populations with discrete generations will tend to oscillate in numbers more than populations breeding continuously; but there is, in a sense, an additional reinforcement of such time-lags in predator-prey systems. In section 3.4.1 we were considering systems in which the food resource remains constant in size (as evidenced by the constancy of the single species' carrying capacity). Now we are

dealing with systems in which both consumer *and* food contribute to the effects of any time-lags. There is, consequently, a tendency for populations of predators and their prey to fluctuate out of phase with one another, and it is essentially this that leads to the 'naive expectation' of coupled predator-prey oscillations outlined in section 5.1. Varley (1947) coined a special term—*delayed density-dependence*—to describe such a relationship between predation-rate and prey density.

### 5.5 Effects on prey fitness

Turning to this next component, we can note that when predators and prey interact, the fitness of prey individuals is obviously affected by the predators, but it is also influenced by the prey themselves through the density-dependent process of intraspecific competition. As Chapters 1–3 made clear, this will tend to regulate the size of a single-species prey population, but in so doing it will also tend to *stabilize* the interaction between the prey and their predators. Prey populations reduced by their predators will experience a compensatory decline in the depressant effects of intraspecific competition; while those that grow large through the rarity of predators will suffer the consequences of intraspecific competition all the more intensely.

The most important effects on prey fitness in the present context, however, are attributable to predators. These can be most easily described in the case of parasitoids and their hosts: a host which is successfully attacked dies—its fitness is reduced to zero. It might appear, moreover, that the effects of true predators on their prey are equally straightforward—and they often are. But consider, by contrast, the work of Errington (1946). Errington made a long and intensive study of populations of the musk-rat (*Ondatra zibethicus*) in the north-central USA. He took censuses, recorded mortalities and movements, followed the fates of individual litters, and was particularly concerned with predation on the musk-rat by the mink (*Mustela vison*). He found that adult musk-rats that were well established in a breeding territory were largely free from mink predation; but those that were



**Fig. 5.7** The relationship between the rate of infection of the water bug *Hydrometra myrae* (host) with the mite *Hydryphantes tenuabilis* (parasite) and (a) host survival, (b) host life expectancy, (c) host maturity, (d) host fecundity, and (e) host rate of increase. (After Lanciani, 1975.)

wandering without a territory, or were exposed by drought, or injured in intraspecific fights were very frequently preyed upon. Certainly, those that were killed had their fitness reduced to zero. Yet, because these were individuals that were unlikely to ever produce offspring, they had low or zero fitnesses anyway. Similar results have been obtained, in fact, for predation on other vertebrates. Those most likely to succumb are the young, the homeless, the sick and the decrepit—the very individuals whose immediate prospects of producing offspring are worst. The harmful effects on the prey population are clearly not as drastic as they might be; and while the effects of true predators on their prey are often straightforward, there are obviously cases, particularly amongst vertebrates, in which the superficial simplicity can be misleading. In particular, a predator that effectively ignores the potential contributors to the next prey generation will have very little effect on prey abundance.

Nevertheless, it is possible in both true predators and parasitoids to equate the predation-rate in a population with the prey death-rate; the difficulty is that prey death does not always lead to simple reductions in the overall vitality of the prey popula-

tion. Conversely with parasites it is well known that the effects on the host are often not drastic (though, of course, to conform with the definition in section 5.1, and thus warrant inclusion in this chapter, the parasite must have some adverse effect on its host's fitness). 'Predation-rate' in parasites, therefore, cannot be equated with host death-rate. Instead, it can be taken as the rate at which host tissue and energy is diverted from hosts to parasites.

Predation-rate in parasites, then, is obviously likely to increase with increases in the mean number of parasites per host; and the effect this can have on host fitness is depicted in Fig. 5.7, illustrating the work of Lanciani (1975) on the ectoparasitic mite, *Hydryphantes tenuabilis*, and its host, the water bug *Hydrometra myrae*. It is clear from Fig. 5.7a & 5.7b that the mite affects the survival of its host, and from Fig. 5.7c & 5.7d that it affects its host's fecundity. Taken all in all, therefore, the mite affects the host's reproductive potential (Fig. 5.7e), and this effect increases with increasing intensity of infection. In other words, the greater the proportion of parasites to hosts, the greater their depressant effect will be; there is inverse density-dependence tending to destabilize the host-parasite interaction.

### 5.5.1 The effects of herbivores on plant fitness

Being primary producers, plants provide food resources and are prey to the attentions of herbivores. Careful examination of natural populations of plants

frequently reveals individuals bearing leaves or stems that have been trimmed and seeds that are bored or cracked open. Such evidence, moreover, may only be conspicuous at particular phases in the life cycle of a plant species. In considering the effects on plants of animals that eat them it is useful to recognize a continuum. At one end, the effect may be the immediate death of the individual plant or seed because of (almost) entire consumption; whilst at the other the effect may be the removal of plant parts with the donor remaining alive and apparently unaffected in terms of its survival and fecundity. In a simple classification we can thus distinguish between, on the one hand, true predators such as granivorous ants (Chapter 2) and frugivorous bats, and on the other hand grazers such as caterpillars that characteristically tend to leave plant meristems from which plant regrowth can occur. Between these end-points lies an array of herbivore effects that may precipitate the earlier death of an individual than would otherwise occur. We might, for instance envisage a plant pathogen reducing the photosynthetic area of an individual to such a degree that its ability to compete with neighbours is lowered and its death hastened.

To seed-eating animals, the crops of seed represent a source of highly nutritious food, which is packaged in a discrete, compact way; and it would be easy to argue that each seed eaten represents a measurable reduction in fitness, since it constitutes the death of a whole individual. It is perhaps more valid, however, to consider not the fitness of the seeds themselves, but the fitness of the parent that produced them. We can see, for instance, in the related case of fruit-eating herbivores, that although a significant quantity of plant material is lost with every fruit eaten, and many seeds (i.e. individuals) are destroyed in the process, the herbivore by acting as an essential agent of seed dispersal is, from the parent plant's point of view, a net contributor to fitness. (Similar comments apply to animal pollinators.) And while the situation is not quite so clear-cut in the case of specialist seed-eaters, there is certainly some evidence to suggest that a parent plant's fitness is not incrementally reduced each time one of its seeds is eaten.

Lawrence and Rediske (1962), for instance, moni-

tored the fates of experimentally sown Douglas fir seeds, both in open plots and in plots supposedly screened from the attacks of vertebrate herbivores. Their results (Table 5.3) indicate that their screening was effective in that vertebrate granivores were largely excluded; but they also illustrate two further points. The first is that these herbivores do, indeed, appear to have an effect on parental output, since the recruitment of seedlings, 1 year after germination, was significantly increased in their absence. The second point, however, is that this effect is rather less than might be expected from a consideration of vertebrate granivores alone. Other sources of mortality, particularly fungal attack at various stages, appear to act in a density-dependent, compensatory fashion. Thus the

Table 5.3 Compensatory mortality when predation is prevented. The fates, in percentage terms, of Douglas fir seeds sown in open and screened plots. (After Lawrence & Rediske, 1962.)

	Plots	
	Open	Screened
<i>Pre-germination period</i>		
Loss due to:		
fungi	19.0	20.1
insects	9.5	12.8
rodents	14.0	1.8
birds	4.1	0.9
unknown	6.8	1.8
Total loss, pre-germination	53.4	37.4
Seeds remaining	46.6	62.6
<i>Germination period</i>		
Non-germinating due to:		
fungal attack	13.1	17.3
seed dormancy	12.7	10.5
Total not germinating	25.8	27.8
Seedlings	20.8	34.8
<i>Post-germination period (1 year after germination)</i>		
Mortality due to:		
fungi	5.4	12.8
other causes	7.3	4.6
Total mortality	12.7	17.4
Seedlings surviving	8.1	17.4

herbivores, like the minks preying on Errington's musk-rats, are, to some extent, removing individuals that are already doomed.

We have, of course, already met a similar example of granivory in section 4.3: Brown and Davidson's (1977) granivorous ants tended to consume seeds that would otherwise have been taken by rodents, and vice versa. Yet the two guilds, together, caused a measurable reduction in the size of the seed population; and since germination and subsequent establishment depends on the occupation of a favourable microsite (which is largely a matter of chance), this, in turn, must have caused a reduction in the size of the populations of adult plants in subsequent generations. Granivores seem, therefore, to adversely affect plants, but not necessarily to the extent suggested by superficial examination. The attractive hypothesis that dispersal of seeds by ants to improved soil close to ant nests has little support from field studies (Rice & Westoby, 1988).

When we turn from seeds and fruits to seedlings and adult plants, the assessment of herbivore damage becomes, if anything, more difficult. The range of responses of growing plants (Table 5.4) in general to the effects of herbivores is considerable and has been the subject of substantial research interest not least for weed biocontrol (Crawley, 1989).

At first sight it might be argued that all of the responses illustrated in Table 5.4 will automatically lead to fitness reductions. For instance metabolic energy and resources diverted towards chemical or mechanical defence might otherwise be used for growth and enhanced survival, and changes in rate of development and re-allocation of resources may lead to reduced fecundity. However, we need to view such responses in context of (i) the coevolution of a plant species and its herbivores; and (ii) knowledge of the key factors acting at each stage in the plant's life cycle that operate in a density-dependent, regulatory manner.

Coevolution might be expected to select for more tolerant plants, less damaging herbivores and more specialist relationships. McNaughton (1983) has proposed that the long-term evolution of plants and herbivores has led to two major groups of terrestrial

Table 5.4 Some examples of plant responses to herbivory

References	
<i>Elicitation of chemical defences</i>	
Induction of tannin and phenol content in leaves after damage	Raup & Tallamy, 1990
<i>Elicitation of mechanical defences</i>	
Increase in density of prickles, spines and hairs on stems after grazing	Kaban & Myers, 1989
<i>Alteration of size, shape and phenology</i>	
Return to juvenile growth form	Bryant, 1981
Change in time of leaf abscission after herbivory	Williams & Whitham, 1986
<i>Sex expression</i>	
Reduced sexual reproduction in <i>Pinus edulis</i>	Whitham & Mopper, 1985
<i>Re-allocation of resources in perennials</i>	
Increased investment in tuber production in <i>Helianthus tuberosus</i> after above-ground flower bud loss	Westley, 1993
<i>Change in rate of growth and development</i>	
Linear and non-linear damage relationships between parameters of plant growth and development and insect population density	Crawley, 1983

plants classified according to 'fundamental botanical attributes, the nature of their present herbivore fauna, and the apparent nature of their long-term coevolutionary relationships with herbivores'. One group, comprising mainly the monocotyledons exhibit growth forms that are likely evolutionary responses to grazing by mammals and orthopterans; plant species may possess short-lived repeating modular units with basal meristems, have high capacity for clonal reproduction and possess general physical defence mechanisms. The other group (consisting of gymnosperms, dicotyledons and non-graminoid monocotyledons) possess more elaborate growth forms, develop from apical rather than basal meristems and commonly display toxic specialist chemical defences, recent evolution having been in association with herbivorous insect taxa. In evolutionary terms then, present observable plant responses may reflect fitness



advantages accrued in response to past selection by herbivores.

On ecological time scales there is evidence for indisputable fitness reduction in some instances. Haines (1975), for instance, obtained frequency distributions of seedling populations in different areas whilst investigating the activities of leaf-cutting ants (*Atta colombica tonsipes*). (These ants cut leaf, flower and fruit material, which is then transported to their nests where the harvested plant material is decomposed by a fungus. The fungus is eaten by the ants, and the degraded plant remains dumped at 'refuse tips'.) The survivorship and size of seedlings of forest plants are inversely related to the frequency of visitation by the ants (Fig. 5.8). Seedlings in parts of the forest away from nests and dumps are present in all size-classes, but on the nests and dumps themselves most of the seedlings present are very small. Thus, the chance of a seedling maturing into the forest canopy appears to be zero if it arises in areas regularly frequented by ants. It is, however, unusual for insect herbivores to cause the death of perennial established plants except in the cases of the deliberate introduction of biological control (Crawley, 1989).

Much more common than the destruction of whole plants is loss of stems or leaves. The consequences of partial defoliation to the subsequent survivorship of a plant are generally difficult to unravel, while the demonstration of proximate death by defoliation is often elusive.

This is because a frequent effect of partial defoliation is to disturb the integrated nature of the whole physiology of the plant. Loss of leaf means not only the loss of photosynthetic area, but also the mobilization of stored reserves for leaf replacement through bud growth; new growth demands protein, carbohydrate and minerals—the high quality components required by predators. Thus, persistent defoliation of young, actively growing leaves may constitute a rapid drain of stored reserves. Moreover, such changes in physiology may result in an alteration in the rate of root growth, and in some cases in root dieback.

A particular feature of species that tolerate grazing is the ability to quickly restore the root to shoot ratios (in biomass) present before grazing started (Piper &

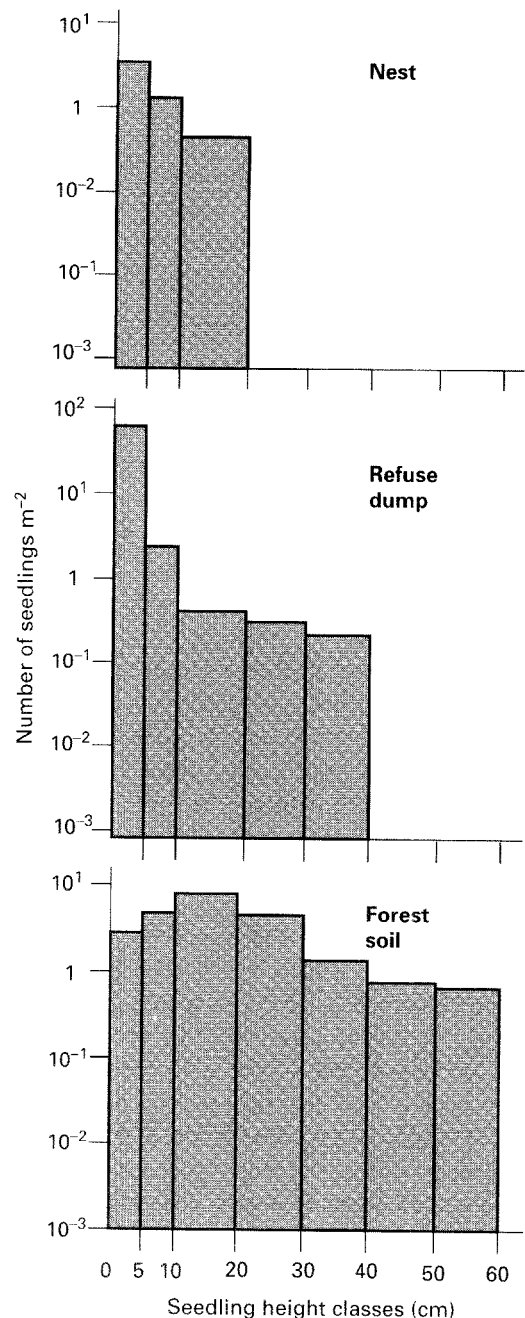


Fig. 5.8 Seedlings do not survive to a large size in the presence of ants. The size-structure of seedling populations in tropical rainforests on nests and refuse dumps of leaf-cutting ants *Atta colombica tonsipes* and on forest soil. The density of seedling height classes are presented. (Data from Haines, 1975.)

Weiss, 1993). Some species are able to increase photosynthesis in the remaining plant in response to defoliation (Gold & Caldwell, 1989) and defoliated plants therefore show a higher relative growth-rate than undefoliated ones. In some cases the increased net primary production can exceed that of control plants, in which case the response has been described as 'overcompensatory', in contrast to those where the net rate is decreased ('undercompensatory'—Archer & Tieszen, 1983). When such production results in the development of new potentially autonomous plants (e.g. shoots in perennials) or overall larger plant size the response has been described as 'herbivore increased fitness'. However there is (i) no clear consensus on the spectrum of plant regrowth patterns that may occur in response to grazing and certainly such responses are dependent on both defoliation history and environment; and (ii) whilst there has been considerable debate that herbivory in principle could increase plant fitness the available evidence suggests that it does not (Belsky, 1986). What is clear is that reductions in photosynthetic area, root volume and stored reserves necessarily place a defoliated individual at a disadvantage in any competitive struggle—a disadvantage that would obviously be intensified still further if buds, the regenerative organs, were subject to predation as well. Competitive disadvantage will result in reduced plant size (see below) which in return will be reflected in fecundity (Rees & Crawley, 1989). The low levels of defoliation that have been observed in natural woodlands has often been assumed to have negligible effects on plant fecundity because of plant compensatory growth processes. To test this, Crawley (1985) examined matched pairs of oak (*Quercus robur*) trees over 4 years; in each pair one tree was regularly sprayed with insecticide to kill all defoliating and sap-sucking insects and the other was sprayed with water. He showed that whilst tree growth (girth) was unaffected by insect exclusion and unsprayed trees lost only 8–12% of their leaf area, sprayed trees consistently produced more seeds (2.5–4.5-fold) than unsprayed ones.

Defoliation may thus have important repercussions on seed production but the time and frequency at which it occurs is also important. Regular removal of

vegetative growth in perennial plants tends to reduce flowering, but the time at which defoliation occurs is critical in determining the actual response of the plant. If the inflorescence is formed prior to defoliation, the response to leaf removal is seed abortion, or for individual seeds to be smaller; whereas defoliation before inflorescence production is likely to halt or severely constrain flower formation. Flower loss itself by insect attack or very high aphid infestations may severely reduce seed production.

Some plant predators do not defoliate their host, but extract food requirements from within the plant. The detailed work of Dixon (1971a, b), for instance, has clearly demonstrated that aphid infestations on lime saplings cause at least a 10-fold reduction in the rate of total dry weight increase (from 7.7 down to 0.6 g week<sup>-1</sup>), even though average and total leaf area per sapling remained unaltered. Yet, examination of the root systems of the infested plants revealed that no growth had occurred below ground subsequent to infestation; and the energetics of this interaction suggest that, on average, 30 aphids per leaf during the growing season is sufficient to completely drain the annual net production of the tree. This average is obviously an oversimplification, but the figure agrees reasonably well with observed natural aphid densities (Dixon, 1971b), implying that although they cause no immediate visual damage, aphids may substantially limit the growth of lime trees, and they may, in consequence, affect survivorship.

Evidence from exclusion experiments point strongly to the indirect effects of herbivory leading to altered competitive abilities in plant communities. From a range of field studies Crawley (1989) concluded that in almost all cases the dominant plant species in a natural community was changed after the deliberate exclusion of vertebrate herbivores accompanied by detectable changes in relative plant abundance; but much less so in studies of insect exclusion.

However, very few critical experiments have been conducted to examine the change in competitive interactions amongst plants experiencing herbivory. In one such study Weiner (1993) deliberately manipulated both herbivore (the snail, *Helix aspersa*) and plant (*Hypochaeris radicata*) density in an experimental

system. Predictably, mean plant size diminished with increasing plant density in the absence of herbivory, indicating intraspecific competition in the plant population. Moreover, mean plant size was further reduced by snail herbivory, the more so the higher the density of snails, but to the same proportional extent at each plant density (i.e. there was no interaction between herbivore and plant population density). Increasing herbivore density did, however, reduce the number of plants surviving to the end of the experiment, mortality being most marked at high herbivore and plant densities. The most conspicuous effects were, however, seen in the size distribution of plants. At low plant density, herbivory reduced the size of many individuals without influencing the larger plants, causing an increase in the inequality of plant sizes in the population. But at high plant density, the main effect of snails was a reduction in surviving plant density with relatively little effect on plant size variation. This one example illustrates some of the subtle effects of herbivory on plants competing in monocultures. If intraplant competition is intense and asymmetric (Chapter 2) herbivory may reduce competition and restrict (or decrease) the resulting size variability that asymmetric competition generates. However, if herbivore attack is size-dependent, then it may amplify asymmetric competitive interactions amongst plants surviving herbivory. (Weiner observed that snails did not feed on large plants grown in isolation reflecting their aversion to feeding in a low cover environment.)

At the present time it remains impossible to generalize on the effects of herbivores on competitive interactions in plant populations due to the lack of detailed experimental study; empirical observations on community changes (Harper, 1977) and theoretical studies (Crawley & Pacala, 1991) strongly suggest that changes in competitive ability may well be mediated by herbivores but the precise processes remain hidden.

Overall, therefore, we can see that there is ample evidence to suggest that the effects of herbivores on both seeds and growing plants may be substantial. The extent to which plant fitness is altered by herbivores, and in turn herbivory, acts as a regulating

factor in plant population dynamics remains to be unequivocally demonstrated.

## 5.6 The effects of predation-rate on predator fitness

### 5.6.1 Thresholds

The effects of predation-rate on predator fitness—like the effects of predation-rate on prey fitness—appear, superficially, to be straightforward; and in the case of parasitoids they certainly are: every host successfully attacked by a parasitoid represents an incremental increase in parasitoid fitness. In all other cases, however, there is an added complication. Predators, herbivores and parasites all require a certain quantity of 'prey' tissue for basic maintenance; and it is only when their intake exceeds this threshold that increases in predation-rate lead to measurably increased benefits to the predator. This is illustrated with typical examples in Fig. 5.9a (predator growth-rate) and Fig. 5.9b (predator fecundity). The consequences of this threshold for the stability of predator-prey interactions are fairly obvious. There is a tendency at low prey densities for predation-rate to fall below the threshold, causing predator fitness to slump to zero. The adverse effects of low prey density on predator

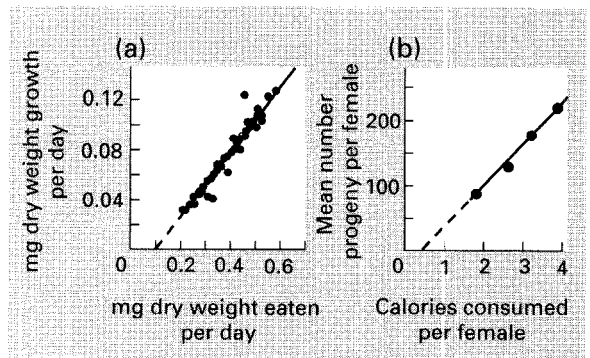


Fig. 5.9 Prey thresholds for predators. (a) Growth in the spider *Linyphia triangularis* (Turnbull, 1962). (b) Reproduction in the water flea *Daphnia pulex* var. *pulicaria* (Richman, 1958). (After Hassell, 1978.) 1 calorie (non-SI unit) = 4.186 joules.

fitness are, therefore, exaggerated, and the interaction generally is *destabilized*.

### 5.6.2 Food quality

There is another factor complicating the relationship between predation-rate and the fecundity and survivorship of predators, however, which itself is of greater importance, namely *food quality*. It is not the case that each item (or even each gram) of food consumed by a predator or herbivore is equivalent. The chemical composition of food, and its accessibility via digestion to the predator, both have a considerable bearing on the way in which food consumption affects predators. This is particularly apparent amongst herbivores (see White, 1978; Lawton & McNeill, 1979).

In particular, herbivores are greatly affected by the nitrogen content of their food. One has only to consider the honeydew (excess carbohydrate) excreted by aphids, to realize that many herbivores must ingest vast quantities of plant tissue in order to consume sufficient amounts of amino acids. Moreover, there is good evidence that herbivore abundance can be limited by nitrogen content (i.e. food quality). Many herbivores only have access to low quality food, and they have insufficient time and energy to digest enough of this to provide them with protein for maintenance, let alone growth and reproduction. This was shown, for instance, by Sinclair (1975) who noted the protein content of the food available to the wildebeest in Serengeti (Tanzania) during 1971, and compared this with the protein content of the food they ate (Fig. 5.10a). He also monitored (Fig. 5.10b) the fat reserves in the bone marrow of live males, and of males that died of natural causes (these reserves being the last to be utilized).

It is clear from Sinclair's results that, despite selecting nitrogen-rich plants and plant-parts, the wildebeests consumed food in the dry season which was below the level necessary even for maintenance (5–6% crude protein); and, to judge by the depleted fat reserves of dead males, this was an important cause of mortality. Moreover, when we consider that during late-pregnancy and lactation (December–May in the wildebeest) the food requirements of females are three

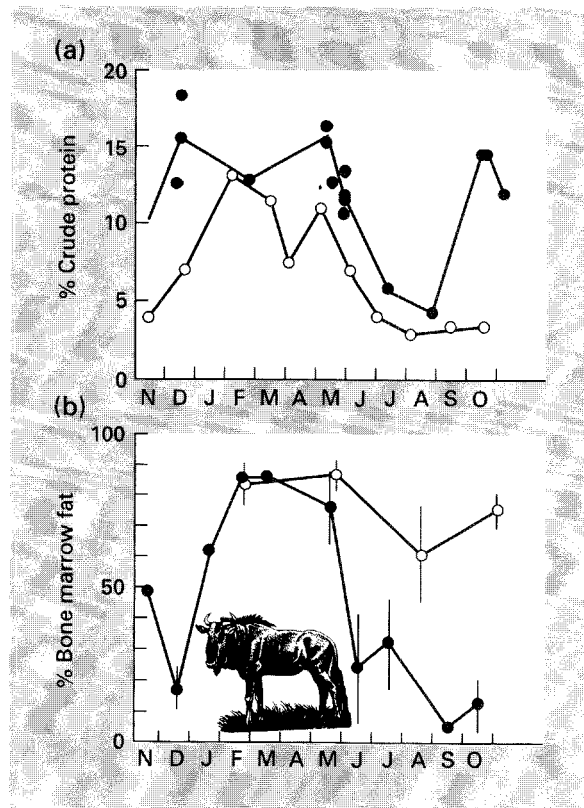


Fig. 5.10 (a) The quality of food measured as crude protein available to (○) and eaten by (●) wildebeest in the Serengeti during 1971. During the dry season, food quality fell below the level for nitrogen balance (5–6% crude protein) despite selection. (b) The fat content of the bone marrow of the live male population (○) and those found dead from natural cases (●). Vertical lines, where present, are 95% confidence limits. (After Sinclair, 1975.)

or four times the normal (Agricultural Research Council, 1965), it becomes obvious that *shortage of high quality food* can have drastic effects on herbivores.

A similar conclusion can be drawn from the work of McNeill (in McNeill & Southwood, 1978). As Fig. 5.11 shows, seasonal peaks in the densities of insects feeding on the grass *Holcus mollis* are related to peaks in food quality (measured as soluble nitrogen) in the leaves and stems—the latter approximating phloem flows to the flowers and developing seeds in the middle of the summer. Once again, food quality

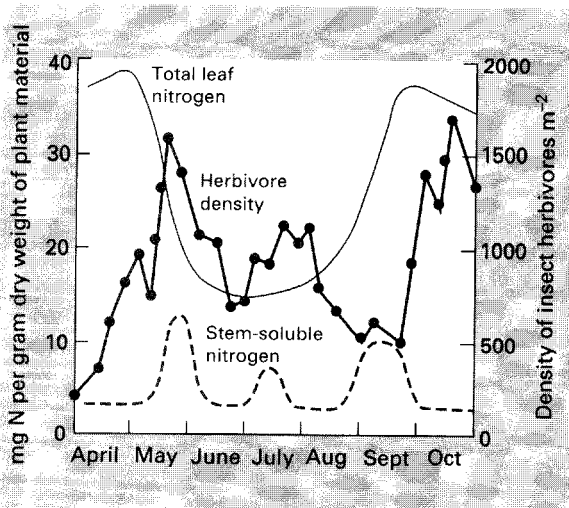


Fig. 5.11 Seasonal changes in the mean numbers of insects on the grass *Holcus mollis* related to changes in food quality in the leaves and stems (McNeill & Southwood, 1978). (After Lawton & McNeill, 1979.)

appears to be having an extremely important effect on predators.

Moreover, plant quality does not only affect herbivores because of what plants lack (in terms of nutrients), but also because of the toxic or digestibility-reducing 'secondary compounds' that many plants contain by way of protection. However, while this may have an important evolutionary effect on herbivores, causing them to specialize, it presumably has relatively little effect on those herbivores that are specifically adapted to feed on the plants producing these compounds (Lawton & McNeill, 1979).

## 5.7 The functional response of predators to prey availability

### 5.7.1 The 'type 2' response

We now turn, for our next component, to the way in which the predation-rate of predators, herbivores or parasitoids is influenced by prey availability, and we begin with the simplest aspect of availability: prey density. A fairly typical response is illustrated in Fig. 5.12, which depicts the numbers of *Daphnia* (of a particular size) eaten during a 24-hour period by

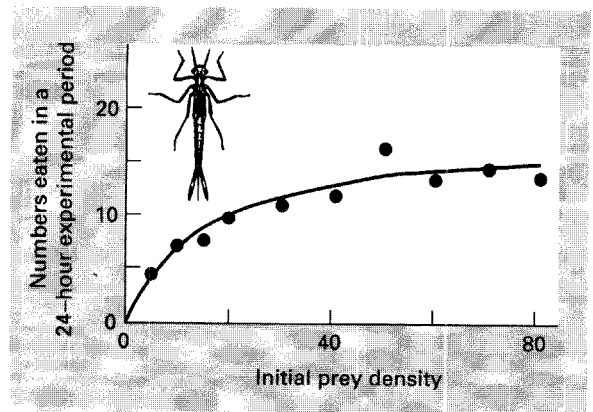


Fig. 5.12 The functional response of tenth-instar damselfly larvae to *Daphnia* of approximately constant size. (After Thompson, 1975.)

tenth-instar larvae of the damselfly *Ischnura elegans* (Thompson, 1975). Figure 5.12 clearly shows that, as prey density increases, the predation-rate responds less and less and approaches a plateau (approximately 16 *Daphnia* per 24-hour period). A similar result is shown in Fig. 5.13 for a herbivore: slugs feeding on *Lolium perenne* (Hatto & Harper, 1969). Such functional responses of predators to changes in prey density were described first by Solomon (1949), but discussed more extensively by Holling (1959), who attributed the form taken by curves like the ones in

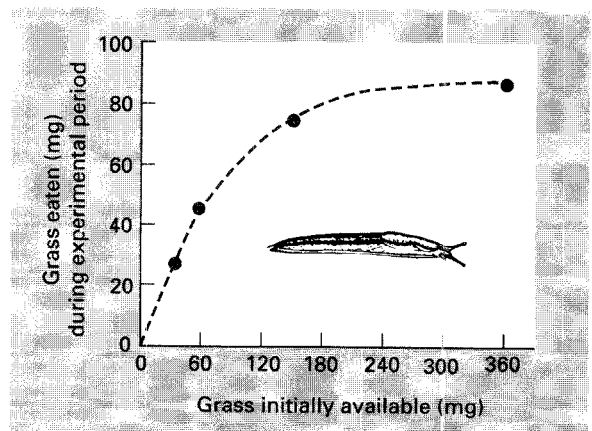
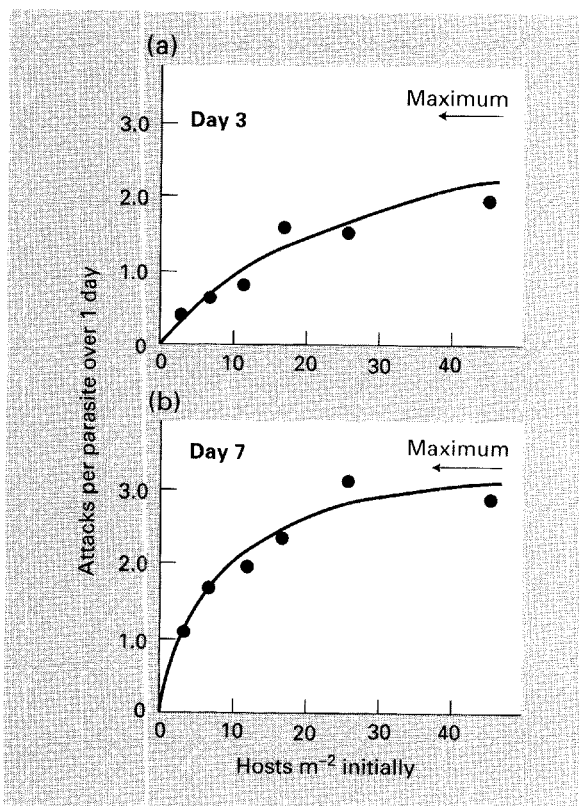


Fig. 5.13 The functional response of single slugs to changes in the amounts of the grass *Lolium perenne* available to be eaten. (Data from Hatto & Harper, 1969.)

Figs 5.12 and 5.13 (which he called 'type 2' responses) to the existence of the predator's *handling time*. (This, as we have seen, is the time the predator spends pursuing, subduing and consuming each prey item it finds, and then preparing itself for further search.) Holling argued that as prey density increases, search becomes trivial, and handling takes up an increasing proportion of the predator's time. Thus, at high densities the predator effectively spends all of its time handling prey, and the predation-rate reaches a maximum, determined by the maximum number of handling times that can be fitted into the total time available.

This view of the type 2 functional response is confirmed and illustrated in Fig. 5.14, which summa-



**Fig. 5.14** The functional responses of the ichneumonid parasitoid *Pleolophus basizonus* to changes in the density of its host *Neodiprion sertifer*; arrows indicate maxima observed in the presence of excess hosts. (a) Parasitoids on their third day, and (b) parasitoids on their seventh day. (After Griffiths, 1969.)

rizes some of the results obtained by Griffiths (1969) in his work on the ichneumonid *Pleolophus basizonus* parasitizing the cocoons of the European pine sawfly, *Neodiprion sertifer*. Taking parasitoids of different ages, Griffiths plotted the number of ovipositions per parasitoid over a range of host densities, but he also calculated the *actual* maximum oviposition-rate by presenting other parasitoids of the same ages with a *superabundant* supply of host cocoons. It is clear from Fig. 5.14 that the type 2 functional response curves did indeed approach their appropriate maxima. Yet, while these maxima (of around 3.5 ovipositions day<sup>-1</sup>) suggest a handling time of around 7 hours, further direct observation indicated that oviposition takes, on average, only 0.36 hours. The discrepancy is accounted for, however, by the existence of a 'refractory period' following oviposition during which there are no eggs ready to be laid. 'Handling time', therefore, includes not only the time actually taken in oviposition, but also the time taken 'preparing' for the next oviposition. Similarly, the handling times suggested by the plateaux in Figs 5.12 and 5.13 will almost certainly include time devoted to activities, peculiar to the damselflies and slugs, other than the direct manipulation of food items. It is in this (non-literal) sense that handling time must be understood.

A further point to note from Fig. 5.14 is that, while the plateau level (and thus the handling time) remains approximately constant with increasing age, the rate of approach to that plateau is much more gradual in the younger parasitoids. In other words, it is apparent that the younger parasitoids search less efficiently, or attack at a slower rate. Thus, at low host densities they oviposit less often than their older conspecifics; but at high densities there is such a ready supply of hosts that even they are limited only by their handling time. Hence, the form taken by a type 2 functional response curve can be characterized simply in terms of a handling time and a searching efficiency (or attack rate); and Hassell (1978) discusses the methods by which these parameters can be obtained from the data. The value of estimating these parameters is illustrated by the work of Thompson (1975) who fed *Daphnia* of a variety of sizes to tenth-instar damselfly larvae (Fig. 5.15). Figure 5.15b shows that the various

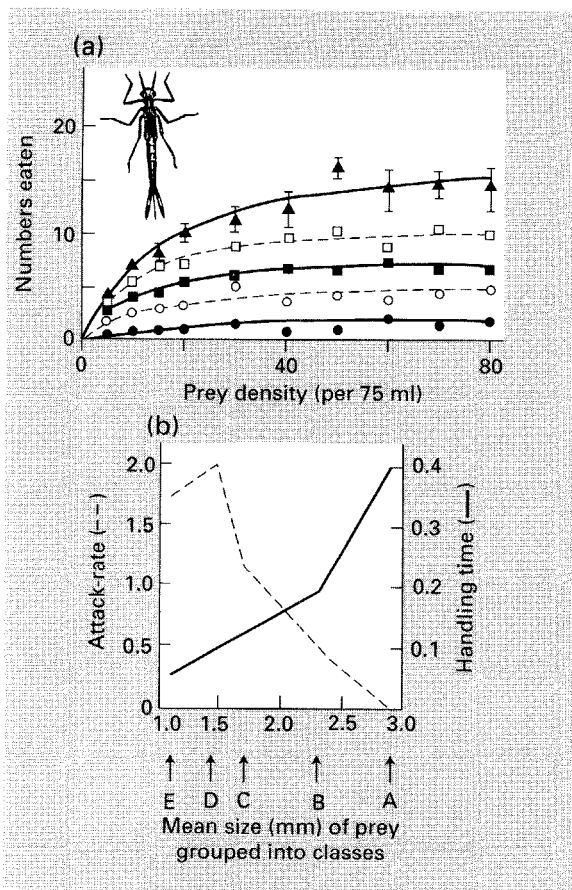


Fig. 5.15 (a) Functional responses of tenth-instar damselfly larvae to *Daphnia* of various sizes. Size A prey (●); B (○); C (■); D (□); E (▲). Standard errors are fitted to the top line. (b) The attack-rates and handling times of these functional responses. (After Thompson, 1975.)

functional responses in Fig. 5.15a are the result of the ways in which both handling time and attack-rate change with prey size. It appears, quite reasonably, that damselfly larvae need more time to handle larger prey, and that they are most efficient and effective at catching *Daphnia* of size D, with attack-rate declining rapidly as prey size increases.

### 5.7.2 The 'type 1' response

A Holling 'type 2' functional response is commonly observed in herbivore-plant, predator-prey and

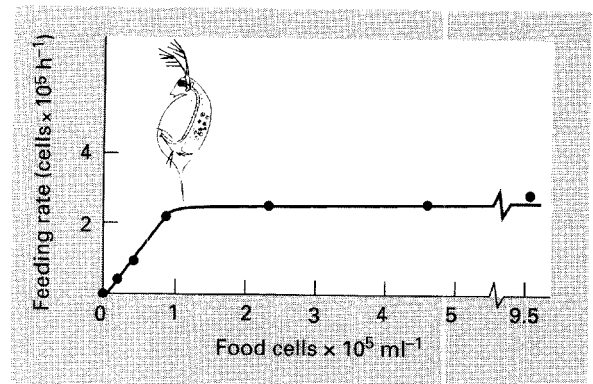


Fig. 5.16 The functional response of *Daphnia magna* to different concentrations of the yeast *Saccharomyces cerevisiae*. (After Rigler, 1961.)

parasitoid-host interactions. Much less common, by comparison, is his 'type 1' response, an example of which is shown in Fig. 5.16. This figure describes work carried out by Rigler (1961) on the feeding-rate of *Daphnia magna* with the yeast *Saccharomyces cerevisiae* as its 'prey'. *Daphnia magna* is a filter feeder, extracting yeast cells at low density from a constant volume of water washed over its filtering apparatus. Below 10<sup>5</sup> yeast cells ml<sup>-1</sup> the predation-rate is directly proportional to the food concentration. But the *Daphnia* must also swallow (i.e. handle) their food. At low concentrations this does not interfere with the predation-rate, because it happens sufficiently quickly to remove all the food accumulated by filtration. Above 10<sup>5</sup> cells ml<sup>-1</sup> however, the *Daphnia* are unable to swallow all the food they filter. At all such concentrations, therefore, they ingest food at a maximal rate, limited by their 'handling' time. The type 1 response is, therefore, an extreme form of the type 2 response in which the handling time exerts its effect not gradually but suddenly.

It is important to note, in both the type 1 and particularly the type 2 response, that the rate of predation on the prey declines as prey density increases. This is, in other words, a case of inverse density-dependence (section 2.6), in which large prey populations suffer proportionately less mortality than small. The consequent effect on the predator-prey interaction is clearly *destabilizing*.

### 5.7.3 Variation in handling time and searching efficiency: 'type 3' responses

It is instructive, at this point, to note explicitly the various components of the handling time and searching efficiency (following Holling, 1965, 1966). Handling time is determined by:

- 1 the time spent pursuing and subduing an individual prey;
- 2 the time spent eating (or ovipositing in) each prey; and
- 3 the time spent resting or cleaning or fulfilling any other essential function (like digestion) prior to the act of predation itself.

Searching efficiency (attack-rate) will depend on:

- 1 the maximum distance at which a predator can initiate an attack on a prey;
- 2 the proportion of these attacks that are successful;
- 3 the speed of movement of the predator and prey (and thus their rate of encounter); and
- 4 the 'interest' taken by a predator in obtaining prey as opposed to fulfilling other essential activities.

We have already seen that at least some of these components are likely to change with predator age (Griffiths, 1969; see Fig. 5.14) and prey size (Thompson, 1975; see Fig. 5.15); and the length of time since the predator's last meal (its hunger) is also likely to modify its response (i.e. its 'interest' in food, and thus its attack-rate, will be altered). Of particular importance, however, is the way in which these components vary with prey density, or, more generally, relative and absolute prey availability.

An example which effectively shows *attack-rate varying with prey density* is illustrated in Fig. 5.17a (Hassell *et al.*, 1977): when host densities are low, the parasitoid *Venturia canescens* spends a relatively large proportion of its time in activities other than probing for larvae (see component 4 above). The consequence of this is shown in Fig. 5.17b (Takahashi, 1968). At low host densities, there is an upward sweep in the functional response curve (Fig. 5.17b, region A), because an increase in density elicits an increased amount of probing and thus an increased effective rate (Fig. 5.17a). Conversely, at higher host densities the attack-rate (as well as the handling time) is relatively

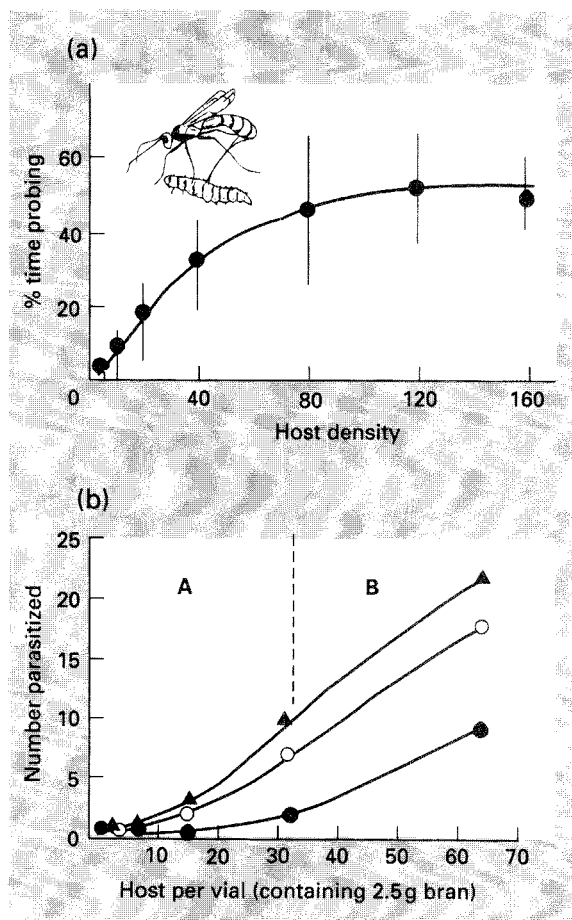


Fig. 5.17 (a) The relationship between the time spent probing by *Venturia canescens* (as a percentage of total observation time) and the density of its host larvae *Plodia interpunctella*. (b) The sigmoidal functional responses of *Venturia canescens* parasitizing *Cadra* larvae of second (●), third (○) and fourth (▲) instars (Takahashi, 1968). (After Hassell *et al.*, 1977.) For further discussion, see text.

constant, leading to the decrease in slope (region B) which is typical of a type 2 response. Overall, the resulting functional response is S-shaped or sigmoidal, and is, in Holling's (1959) terminology, 'type 3'. Clearly it will occur whenever attack-rate increases or handling time decreases with increasing prey density.

### 5.7.4 Switching and 'type 3' responses

There are other (related) circumstances, however,



which will also lead to a type 3 functional response. These are the cases of predator switching considered in section 5.3.2. The resemblance between Fig. 5.17b and Fig. 5.4a and 5.5a is obvious. The major difference is that in the latter case there were two types of prey (rather than one), so that the numbers of prey eaten varied with relative prey availability; we cannot be sure that a type 3 functional response would have resulted had the alternative prey been absent. Nevertheless, the effective result of predator switching is a type 3 functional response: the numbers of prey consumed varies with prey density in a sigmoidal fashion.

Type 3 functional responses, then, resulting from switching or from changes in handling time or attacking efficiency, can occur in predators, parasitoids or herbivores; although it remains to be seen how common and widespread they are. Whenever and for whatever reason they occur, however, the effect on the stability of the interaction will be essentially the same. Throughout region A (Fig. 5.17b)—the upward-sweeping part of the curve—increases in prey density lead to increases in the predation-pressure on the prey: the process is *density-dependent*. It can, therefore, have a potentially important *stabilizing* effect on the inter-

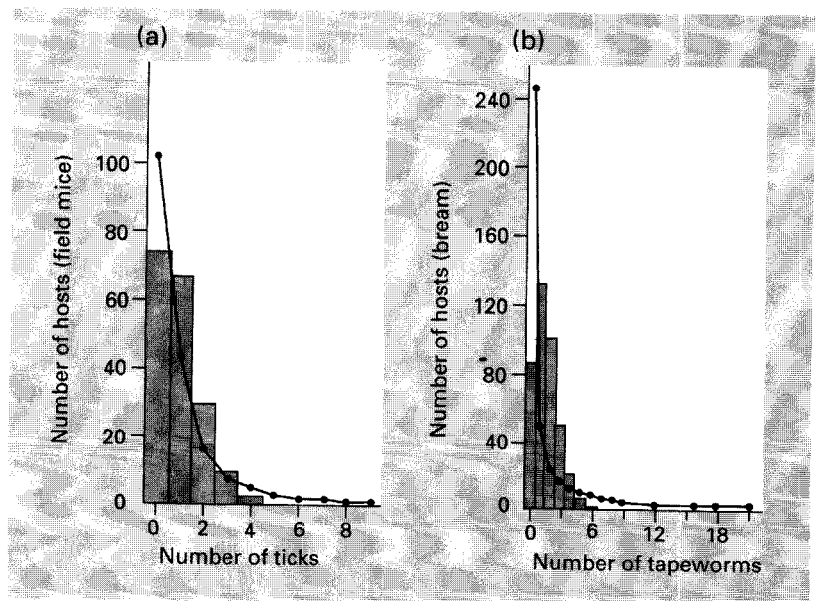
action. The *actual* importance, however, depends on:  
 1 the concavity of the curve in region A; and  
 2 the relevance of the prey densities in region A to a particular field (or laboratory) situation.

## 5.8 Aggregated effects

### 5.8.1 Parasite–host distributions

It was established in section 5.3.2 that polyphagous predators, by exhibiting preferences, distribute their ill-effects unevenly between prey species. We turn now to the distribution of these ill-effects *within a single species of prey*. Consider, to begin with the distributions of parasites on their hosts shown in Fig. 5.18. In both examples, the observed patterns have been compared with the patterns that would have arisen if the parasites had been distributed at random. Random distributions are the simplest imaginable arrangements in that they occur when all hosts and all parasites are equivalent and independent. (An 'even' distribution would only occur if the parasites positively avoided one another.) Yet the observed patterns are far from random. Instead they are distinctly 'clumped'. There are more hosts than expected

Fig. 5.18 The aggregated distributions of parasites on hosts (points and curve), compared to a random distribution (histograms). (a) Ticks *Ixodes trianguliceps* on the wood mouse *Apodemus sylvaticus* (data from Randolph, 1975). (b) Tapeworms *Caryophyllaeus laticeps* in the bream *Abramis brama*. (Data from Anderson, 1974.)



supporting large numbers of parasites, but also more than expected with no parasites at all. In effect, there is a *partial refuge* for the host: the pattern of distribution ensures that an 'unexpectedly' large number of hosts escape parasitization.

Such patterns are extremely common amongst parasites, and, although proposals for underlying mechanisms are usually speculative (Anderson & May, 1978), the effects these patterns have on host-parasite dynamics are fairly obvious. By leaving a large number of hosts unparasitized, even at high levels of infection, the distributions ensure that the host populations are buffered from the most drastic effects of the parasites. This, in turn, tends to ensure that the parasite population has a population of hosts to live on. The basic effect of this partial refuge, then, is to *stabilize* the interaction.

### 5.8.2 Refuges

Partial refuges, as we shall see, are of considerable importance in a wide variety of predator-prey interactions. Yet there are, in some cases, not partial but total refuges, and these can be of two types.

The first is a refuge for a *fixed proportion* of prey. The parasitoid *Venturia canescens*, for instance, when attacking caterpillars of flour moths (*Ephestia* spp.) can

only extend its ovipositor a certain distance into the flour medium. A proportion of the caterpillars—those lying deeply enough to be beyond the ovipositor's reach—are therefore protected in an effective refuge (Hassell, 1978).

In the second type of total refuge, by contrast, a *fixed number* of prey are protected. This is illustrated by Connell's (1970) work on the barnacle, *Balanus glandula*, in which he found that adults are restricted to the upper zones of the shore, while juveniles are distributed throughout a much broader region (Fig. 5.19). This occurs because in the upper zones there are two exposures to the air at low tide almost every day, which means that the whelks that consume the juvenile barnacles in the lower regions—even *Thais emarginata* (Fig. 5.19)—have only two short, high-tide periods to feed (as opposed to a single long one at lower levels). And this is never long enough to find and eat an adult *Balanus glandula* in the upper regions. Thus, the *B. glandula* individuals which the upper zones can support are protected from predation, irrespective of *Thais* numbers. There is a fixed-number refuge.

From what has already been noted about partial refuges, it is clear that total refuges will tend to *stabilize* predator-prey interactions; but it should be equally clear that the (density-independent) fixed-

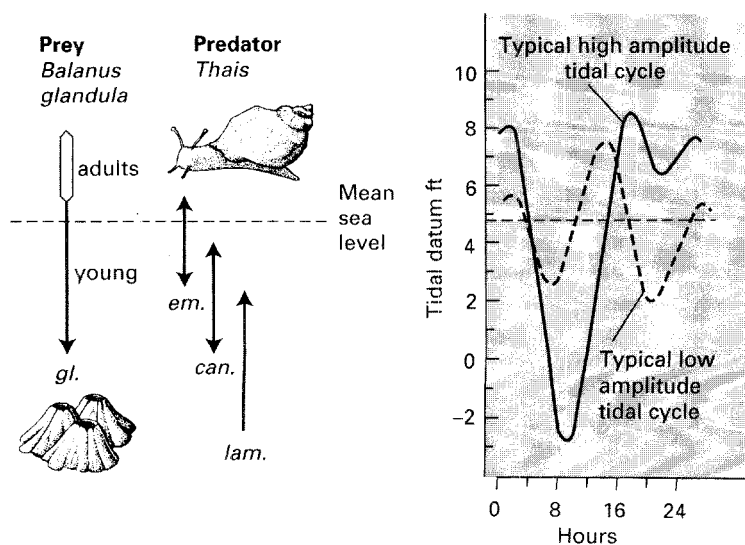


Fig. 5.19 Vertical distributions of barnacle prey (*Balanus glandula*) and whelk predators (*Thais emarginata*, *Th. canaliculata* and *Th. lamellosa*) in relation to typical tidal fluctuations of large and small amplitude. (After Connell, 1970.) For further discussion, see text.

proportion refuge will be much less potent than the (density-dependent) fixed-number refuge, since in the latter case the proportion protected increases as prey density decreases.

### 5.8.3 Partial refuges: aggregative responses

In the living world as a whole, total refuges are probably rather rare. Considerably more common, however, is a tendency for prey to be affected by their herbivores, parasitoids or predators in much the same way as hosts are affected by their parasites (see Fig. 5.18): the ill-effects are aggregated so that the prey have a partial refuge. We can illustrate this, initially, in a herbivore—the cabbage aphid, *Brevicoryne brassicae*. This species, an important pest of cabbage and its relatives, has a marked tendency to form aggregates at two separate levels: nymphs, when isolated experimentally on the surface of a single leaf, quickly form large groups; while populations on a single plant tend to be restricted to particular leaves (Way & Cammell, 1970). The effects are illustrated by an experiment (Way & Cammell, 1970) in which eight small cabbage plants were each artificially infested by 16 aphid nymphs. Four of the eight plants had all 16 nymphs on a single leaf (the normal situation), while the other four had four nymphs on each of the four leaves. Aphid-free leaves were protected from cross-infestation, and colonization by 'outside' aphids was prevented. Productivity was measured by the numbers and weights of adult aphids subsequently produced. Although the differences are small (Table 5.5), it is clear that the normal, aggregated situation, with a single leaf colonized, is the more productive in terms

of aphids. Moreover, the uninfested leaves of the 'one-leaf colonized plants' were healthy at the end of the experiment, while the 'four-leaf colonized plants' were virtually dead. The aphids' behaviour, therefore, does more than increase their own productivity: it also provides a partial refuge for the cabbages. Thus, as a by-product of the aphids' behaviour, many more leaves escape destruction than would do so if the aphids were randomly distributed. The cabbage population is partially buffered from the aphids' ill-effects, and the interaction is (relatively) *stabilized*.

Of course, the aggregated cabbage aphids are themselves the prey of other animals and, indeed, their distribution is typical of the 'patchiness' of prey animals generally. The responses of a predator and a parasitoid to their distribution are shown in Fig. 5.20. In both cases (over at least part of the density range) the time spent on a leaf increases with the density of aphids on that leaf. Thus, if we make the reasonable assumption that an increased searching time leads to an increased proportion of the leaf being searched, which leads to an increase in the proportion of aphids attacked, then clearly the aphids at the lower densities have a smaller probability of being attacked. Once again, therefore, there is a partial refuge, but this time it is the aphids themselves that are protected: aphids in low-density aggregates are most likely to be ignored. (It is important to note, however, that such effects apply only to those parts of the density axis in which 'time spent' increases. The importance of the effects depends on the relevance of these densities in nature.)

Most herbivores, predators and parasitoids appear capable of exhibiting an 'aggregative response', concentrating their ill-effects on a particular portion or patch of their prey population; and by providing a partial refuge for the prey this tends to stabilize the interaction. But it must be realized that in each case this is essentially a by-product of the response (albeit an extremely important one): there is no question of evolution favouring stable populations. This fundamental point is illustrated in Table 5.5 and Fig. 5.20. The predator and the parasitoid concentrate on particular patches (leaves) and make their individual search more profitable; the aphids aggregate in

Table 5.5 Weights of winged adult cabbage aphids produced on small cabbage plants. (From Way & Cammell, 1970.)

	Mean weight of adults at time of peak production (mg) ( $\pm$ SE)	Mean biomass of adults per plant (mg)
One leaf colonized	0.224 $\pm$ 0.012	620
All leaves colonized	0.178 $\pm$ 0.009	578

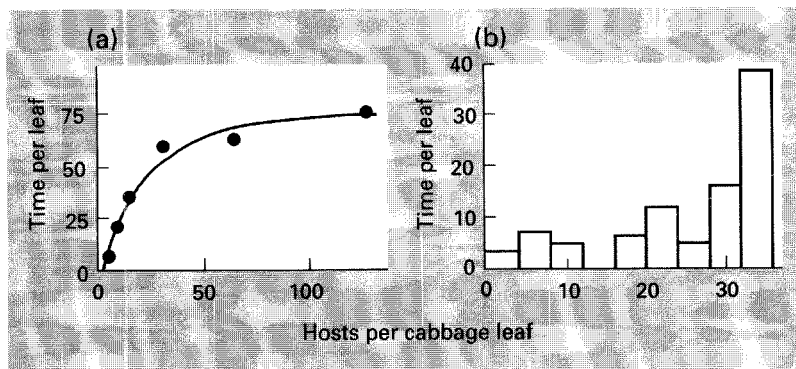


Fig. 5.20 Aggregative responses by a parasitoid and a predator of the cabbage aphid *Brevicoryne brassicae*. (a) Searching time of the braconid *Diaeretiella rapae* at different densities of its host (Akinlosotu, 1973). (b) As (a) but using coccinellid larvae *Coccinella septempunctata*. (After Hassell, 1978.)

patches supporting other aphids and increase their individual productivity. In all cases, the aggregative behaviour is *advantageous to the consumer*.

These data also provide further support for the assertion that *predators choose profitable prey* (in this case, profitable patches). Experimental illustration of this is provided for a two-patch situation by the work of Krebs *et al.* (1978). Great tits were offered rewards (food) at two different perches (patches), but the profitabilities of the two perches were unequal. After a period of learning, the birds concentrated (almost exclusively) on the more profitable patch (Fig. 5.21).

#### 5.8.4 Further responses to patchiness

Of course, by blandly asserting that consumers concentrate on profitable patches we beg the question of what actually constitutes a patch. In the examples shown in Fig. 5.20, for instance, the aphids' predators and parasitoids appear to treat each leaf as a patch; while in the further examples in Fig. 5.22 (which once again show concentration on profitable 'patches') the term 'patch' applies to a whole plant in the case of the braconid *Apanteles glomeratus* (Fig. 5.22a), and simply to a unit area in the case of the ichneumonid *Dia. romus pulchellus* (Fig. 5.22b). Similarly, while the cabbage aphid appears to treat a leaf (or part of a leaf) as a patch, the appropriate scale for many herbivores is the whole plant. One example of this is the moth *Cactoblastis cactorum*, which has been used in Australia to control the prickly pear cacti *Opuntia inermis* and *O. stricta*. *Cactoblastis cactorum* and its food plants now

live at an apparently stable low level of abundance, which can be explained in terms of aggregation by considering some of the results obtained by Monro (1967) for *C. cactorum* and *Opuntia inermis* (Table 5.6). The distribution of *Cactoblastis cactorum* egg-sticks (each containing 70–90 eggs) on prickly pears is distinctly clumped, and the very limited mobility of the larvae means that the 'unexpectedly' high number of

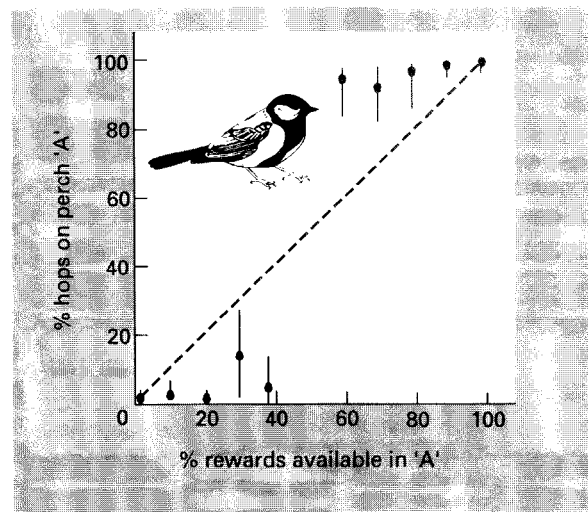


Fig. 5.21 When great tits are faced with a choice of two perches to obtain food, they go for the one with the higher reward rate. The ordinate shows the percentage of responses on one of the perches, and the abscissa is the percentage of rewards available (Krebs *et al.*, 1978). (After Krebs, 1978.) (Geometric means and 95% confidence limits are shown.)

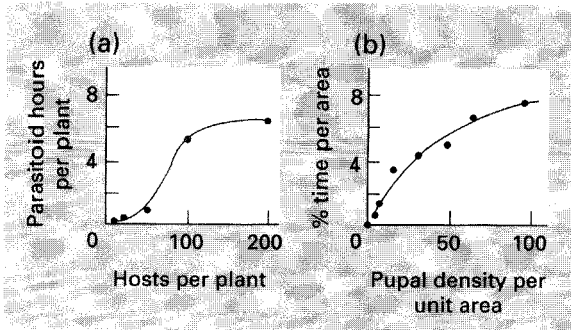


Fig. 5.22 Aggregative responses of (a) the braconid *Apanteles glomeratus* to plants of different *Pieris brassicae* density (Hubbard, 1977), and (b) the ichneumonid *Diadromas pulchellus* to different densities of leek moth pupae per unit area (Noyes, 1974). (After Hassell, 1978.)

plants without eggs are indeed protected. Moreover, the interaction is also stabilized by the death of larvae on plants with too many egg-sticks (roughly more than two per plant). These plants become 'overloaded': they are completely destroyed by the dense aggregation of sedentary larvae, but the larvae themselves then have insufficient food to complete development. This,

Table 5.6 Aggregation in a plant-herbivore interaction. Comparison of observed distributions of *Cactoblastis* egg-sticks per *Opuntia* plant with corresponding Poisson distributions. (After Monro, 1967.)

Site	Mean density (egg-sticks/ segment)	Egg-sticks/plant		Comparison of distribution with Poisson distributions of the same mean by $\chi^2$ test
		Mean	Variance	
1	0.398	2.42	6.16	$p < 0.001^*$
2	0.265	2.09	22.40	$p < 0.001^*$
3	0.084	1.24	5.09	$p < 0.001^*$
4	0.031	0.167	0.247	$p > 0.005^\dagger$
5	0.112	0.53	1.47	$p < 0.01^*$
6	0.137	1.97	18.76	$p < 0.001^*$
7	0.175	0.62	3.55	$p < 0.001^*$
8	0.112	0.34	0.90	$p < 0.05^*$

\*Egg-sticks more clumped than expected for random oviposition.

†Egg-sticks not distributed differently from random.

therefore, is an extreme example of a widespread phenomenon: the predators' ill-effects are aggregated, tending to stabilize the interactions between them and their prey.

### 5.8.5 'Even' distributions

Parenthetically within this component of the interaction, it must be stressed that not all 'predator-prey' distributions are clumped. Indeed, Monro (1967) provides a striking example of a herbivore going to the other extreme. Figure 5.23 shows the distribution of ovipositions by the trypetid fruitfly *Dacus tryoni* in ripe loquat fruit, and also provides an 'expected' random distribution for comparison. It is obvious that the fly spreads its ill-effects much more evenly than expected, so that there are relatively few fruits that escape and few that are overcrowded. Once again, however, as in most of the clumped examples, we can see that the fundamental basis of the pattern is that it is *advantageous to the consumer*—in this case as a result of the

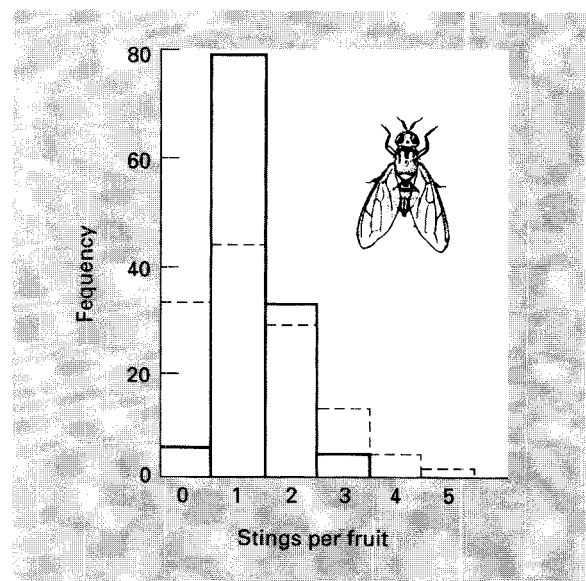


Fig. 5.23 An 'even' distribution: the observed distributions of oviposition stings made by the fruitfly *Dacus tryoni* on loquat fruit (—) compared to an expected random distribution (---) (After Monro, 1967.)

reduction in intraspecific competition experienced by each larva.

### 5.8.6 Underlying behaviour

There are various types of behaviour underlying the aggregative responses of predators, but they fall into two broad categories: those involved with the location of prey patches, and those that represent the response of a predator once *within* a prey patch. Within the first category we can include all examples of predators perceiving, at a distance, the existence of heterogeneity in the distribution of their prey. Rotheray (1979), for instance, found that the parasitoid *Callaspidia defonscolombei* was attracted to concentrations of its syrphid host by the odours produced by the syrphids' own prey: various species of aphid.

Within the second category—responses of predators within prey patches—there are three distinct types of behaviour. The first is illustrated in Fig. 5.24: a female predator of one generation tends to lay her eggs where there are high densities of prey so that her relatively immobile offspring are concentrated in these profitable patches. This response, as far as the predatory individuals themselves are concerned, is essentially passive. By contrast, the second type of behaviour involves a change in a predator's searching pattern in

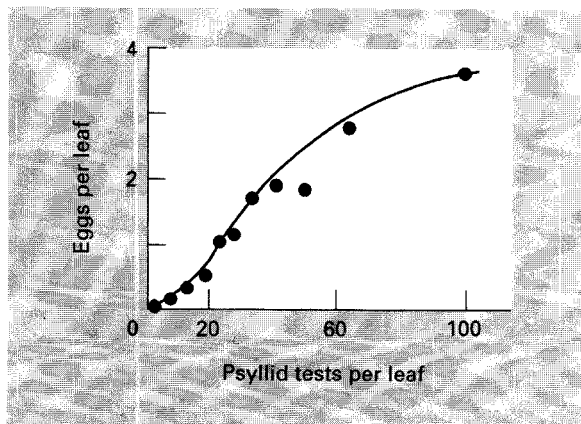


Fig. 5.24 Distribution of *Syrphus* eggs in relation to the number of tests of the psyllid *Cardiaspina albipuncta* per leaf surface (Clark, 1963). (After Hassell, 1978.)

response to encounters with prey items. In particular, there is often an increased rate of predator turning immediately following an intake of food, which leads to the predator remaining in the vicinity of its last food item. Increased turning causes predators to remain in high density patches of food (where the encounter- and turning-rates are high), and to leave low density patches (where the turning-rate is low). Such behaviour has been demonstrated in a number of predators, and is illustrated in Fig. 5.25 for coccinellid larvae feeding on aphids (Banks, 1957).

The third type of behaviour is demonstrated by the data in Table 5.7 (Turnbull, 1964), referring to the web-spinning spider *Archaearenea tepidariorum* preying on fruit flies in a large experimental arena. The spiders tend, simply, to abandon sites at which their capture-rate is low, but remain at sites where it is high. In this case, therefore, the spiders modify their leaving-rate (rather than their turning-rate) in response to prey encounters, but the result, once again, is that predators congregate in patches of high prey density.

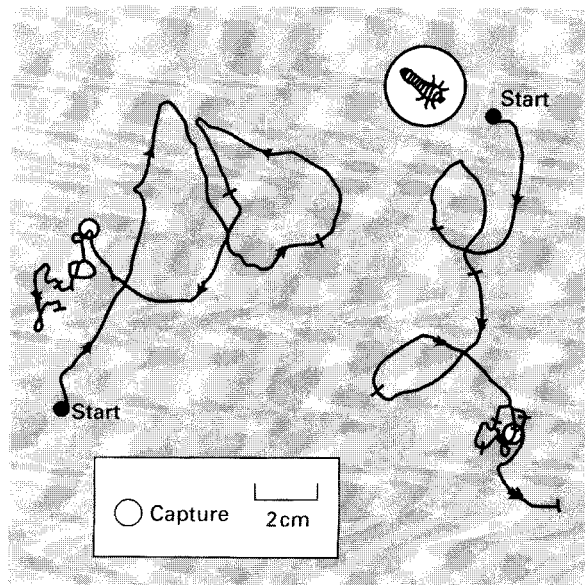


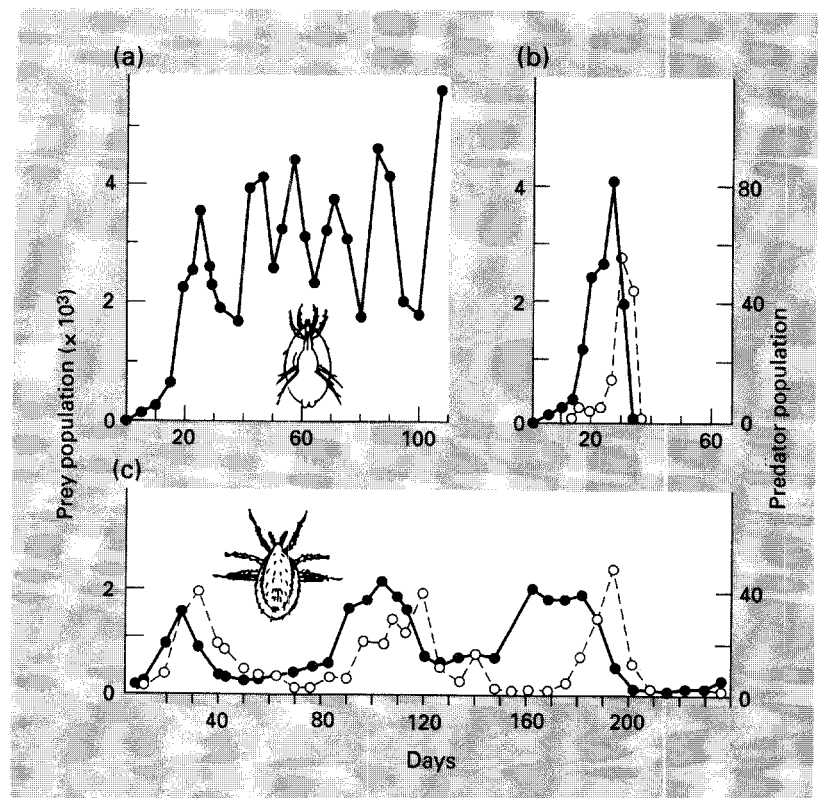
Fig. 5.25 Search paths of hungry, fourth-instar coccinellid larvae before and after capture of a prey (small circle on the path). The rate of turning markedly increases after prey capture (Banks, 1957). (After Curio, 1976.)

**Table 5.7** Site occupation and feeding-rate of spiders feeding on *Drosophila* in an experimental arena with sites of varying suitability for *Drosophila*. (After Turnbull, 1964.)

	Spider					
	1	2	3	4	5	6
Number of sites occupied temporarily	3	2	1	2	4	3
Mean number of days temporary site occupied	2.7	3	5	3.5	3	3
Number of days final site occupied	12	14	15	13	8	11
Mean flies eaten per day at temporary site	0.5	0.2	0	0.1	0.3	0.5
Mean flies eaten per day at final site	3.5	3.4	2.3	2.5	3.4	3.5

### 5.8.7 'Hide-and-seek'

We have seen, then, that the distributions of predators and prey can have important effects on predator-prey dynamics, because predators tend to concentrate on profitable patches of prey. There is, however, in some cases, another perspective from which this behaviour can be seen: predators and prey can appear, in effect, to play 'hide-and-seek'. The most famous and illustrative example of this is provided by the experimental work of Huffaker (1958) and Huffaker *et al.* (1963). Their laboratory microcosm varied, but basically consisted of a predatory mite, *Typhlodromus occidentalis*, feeding on a herbivorous mite, *Eotetranychus sexmaculatus*, feeding on oranges interspersed amongst rubber balls in a tray. In the absence of its predator, *Eotetranychus* maintained a fluctuating but persistent population (Fig. 5.26a); but if *Typhlodromus* was added during



**Fig. 5.26** Predator-prey interactions between the mite *Eotetranychus sexmaculatus* (●) and its predator *Typhlodromus occidentalis* (○). (a) Population fluctuations of *Eotetranychus* without its predator, (b) a single oscillation of predator and prey in a simple system; and (c) sustained oscillations in a more complex system (Huffaker, 1958). (After Hassell, 1978).

the early stages of prey population growth, it rapidly increased its own population size, consumed all of its prey and became extinct itself (Fig. 5.26b). The interaction was exceedingly unstable, but it changed when Huffaker made his microcosm more 'patchy'. He greatly increased its size, but kept the total exposed area of orange the same; and he partially isolated each orange by placing a complex arrangement of Vaseline barriers in the tray which the mites could not cross. However, he facilitated the dispersal of *Eotetranychus* by inserting a number of upright sticks from which they could launch themselves on silken strands carried by air currents. The overall result was a series of sustained and relatively stable predator-prey oscillations (Fig. 5.26c), probably generated by the following mechanism. In a patch occupied by both *Eotetranychus* and *Typhlodromus*, the predators consume all the prey and then either disperse to a new patch or become extinct. In a patch occupied by the predators alone, there is usually death of the predators before their food arrives. But in patches occupied by the prey alone, there is rapid, unhampered growth accompanied by some dispersal to new patches. Dispersal, however, is much easier for the prey than it is for the predators. The global picture is, therefore, a mosaic of unoccupied patches, prey-predator patches doomed to extinction, and thriving prey patches; with some prey and rather fewer predators dispersing between them. While each patch is ultimately unstable, the spatially heterogeneous whole is much less so. Once again, therefore, patchiness has conferred stability; and, in the context of this section, we can see that this example illustrates the effect of temporary 'temporal refuges'.

A rather similar, and ultimately more satisfying example (since it comes from the field), is provided by the work of Landenberger (1973; in Murdoch & Oaten, 1975), who studied the predation by starfish of mussel clumps off the coast of southern California. Clumps which are heavily preyed upon (or are simply too large) are liable to be dislodged by heavy seas so that the mussels die: the predators are continually driving patches of prey to extinction. Yet the mussels have planktonic larvae which are continually colonizing new locations and initiating new clumps. Conversely,

the starfish disperse much less readily. They tend to stay wherever the clumps are, and there is a time-lag before they leave an area when the food is gone. The parallel with Huffaker's mites is quite clear: patches of mussels are continually becoming extinct, but other clumps are growing prior to the arrival of starfish. The starfish show aggregative behaviour, concentrating on large, profitable clumps, and allowing the initially small, protected clumps to become large and profitable themselves. 'Hide-and-seek' and aggregative behaviour are, therefore, essentially indistinguishable, and both illustrate the important stabilizing effects of aggregation on the predator-prey interaction.

We have one further, important aspect of this 'aggregative behaviour' component to consider, but before we do so it is necessary to examine another component: the interactions that occur *between* predators.

### 5.9 Mutual interference amongst predators

Predators commonly reserve particular aspects of their behavioural repertoire for interactions with other predators of the same species: herbivorous (nectar-feeding) humming-birds, for instance, actively defend rich sources of food (Wolf, 1969); badgers patrol and visit the 'latrines' around the boundaries between their territories and those of their neighbours; and females of *Rhyssa persuasoria*, an ichneumonid parasitoid of wood wasp larvae, will threaten and, if need be, fiercely drive an intruding female from the same area of tree trunk (Spradbery, 1970). On a more quantitative level Kuchlein (1966) has shown that an increase in the density of the predatory mite *Typhlodromus longipilus* (and thus an increase in the number of predator-predator encounters) leads to an increase in the rate of emigration from experimental leaf discs containing prey mites; and a similar situation is shown for a parasitoid of leek moth pupae in Fig. 5.27. In both qualitative and quantitative examples, then, the essential effect is the same: the time available to the predator (or herbivore or parasitoid) for 'prey'-seeking is reduced by encounters with other predators. And the importance of this effect increases with predator



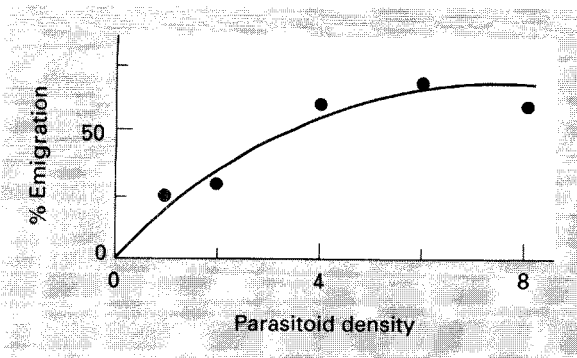


Fig. 5.27 The effect of female parasitoid density on parasitoid emigration from an experimental cage; the ichneumonid *Diadromus pulchellus* (Noyes, 1974). (After Hassell, 1978.)

density, because this increases the rate of predator–predator encounters.

The precise characteristics of such *mutual interference* will vary from species to species, but all examples can be reduced to a common form in the following manner (Hassell & Varley, 1969; Hassell, 1978). The *end-result* of mutual interference is that each predator

consumes less than it would otherwise do. Consumption-rate *per predator* will, therefore, decline with increasing predator density. Thus, if we ignore the fact that search time is reduced by mutual interference as predator density increases (i.e. assume that search time remains constant), it will *appear* as if searching (or attacking) *efficiency* is declining. Mutual interference can then be demonstrated by plotting apparent attacking efficiency (calculated from data on consumption-rates on the assumption of *random search*: see section 5.10) against predator density. This has been done in Fig. 5.28, on logarithmic scales. As expected, the slope in all cases is negative, and may be denoted by  $-m$ , where  $m$  is termed the *coefficient of interference*. The general form of this relationship is probably represented by Fig. 5.28a & 5.28b, in which  $m$  remains constant at high and moderate predator densities, but decreases at low densities. This indicates that apparent attacking efficiency cannot continue to rise as predators become increasingly scarce (moving from *right to left*). As Fig. 5.28c–e shows, however, the coefficient of interference often remains constant throughout the range of densities actually examined.

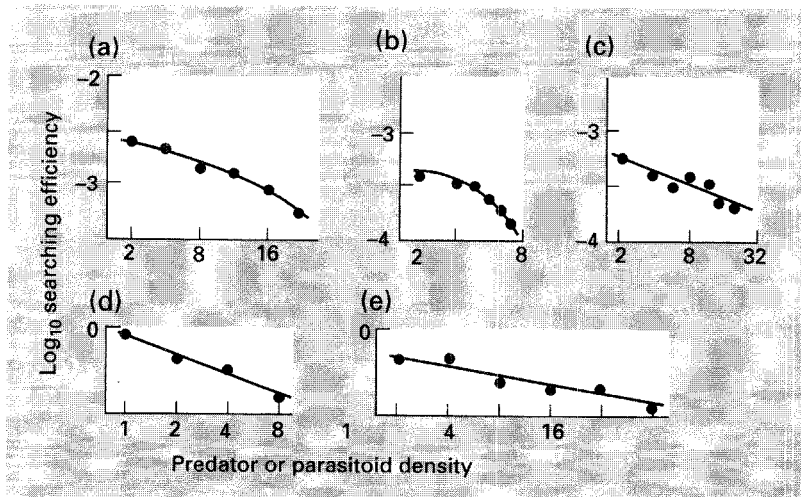


Fig. 5.28 Interference relationships between the searching efficiency (log scale) and density of searching parasitoids or predators. (a) *Encarsia formosa* parasitizing the whitefly *Trialeurodes vaporariorum* (Burnett, 1958). (b) *Chelonus texanus* parasitizing eggs of *Anagasta kühniella* (Ulyett, 1949b). (c) *Cryptus inornatus* parasitizing cocoons of

*Loxostege stricticalis* (Ulyett, 1949a). (d) *Coccinella septempunctata* feeding on *Brevicoryne brassicae* (Michelakis, 1973). (e) *Phytoseiulus persimilis* feeding on deuteronymphs of *Tetranychus urticae* (Fernando, 1977). (After Hassell, 1978.)

This important observation will be utilized in section 5.13.

We have just seen that as a result of mutual interference amongst predators, attacking efficiency decreases as predator density increases. There is, in other words, a density-dependent reduction in the consumption-rate per individual, and thus a density-dependent reduction in predator fitness, which will have a *stabilizing* effect on the predator-prey interaction. The coefficient of interference,  $m$ , is a measure of this stabilizing effect.

### 5.9.1 A similar effect amongst parasites

Interestingly, although parasites are not subject to the same sort of mutual interference as predators, herbivores and parasitoids, they are affected by another process which has a rather similar result. Immunological responses by hosts can play an important role in parasite mortality, and the strength of the response is often directly related to the size of the parasite burden. Thus, the probability of host-induced parasite mortality will increase with greater parasite density, as Fig. 5.29 illustrates. There is no direct interference, of course, but an individual parasite's fitness is reduced

by the presence of other parasites. Once again, therefore, the general effect is to *stabilize* the interaction (see Anderson & May, 1978).

### 5.10 Interference and pseudo-interference

We can return now to aggregative behaviour, and consider an important alternative approach to its effects. This was introduced in a mathematical way by Free *et al.* (1977); but for our purposes their ideas can be discussed verbally. By concentrating on profitable patches, a single predator increases the number of prey it eats per unit time; the same predator searching randomly would eat less. This means that the apparent attacking efficiency (calculated from consumption-rates on the *assumption* of random search) is higher in the 'aggregated' predator. Yet the same predator, by removing prey from the profitable patches, will marginally reduce the profitability of those patches. This, in time, will make aggregated search more like random search, and the apparent attacking efficiency will decline. And if there are many predators, all concentrating on profitable patches, then this decline may be immediately perceptible. Thus, in general, we can expect the apparent attacking efficiency to decrease as predator density increases. Yet this is the very relationship that we saw resulting from mutual predator interference in the previous section. In the present case, therefore, this *consequence of aggregative behaviour* may be described as 'pseudo-interference' (Free *et al.*, 1977).

The importance of pseudo-interference, along with the nature of mutual interference itself, is amply illustrated in the following example (Hassell, 1971a, b, 1978) in which larvae of the flour moth *Ephesia cautella* were parasitized by *Venturia canescens*. The larvae were confined in small containers at densities ranging from four to 128 per container, and exposed to one, two, four, eight, 16 or 32 parasitoids for 24 hours. Line A in Fig. 5.30a was obtained in the manner of the previous section (by counting the total number of hosts parasitized and assuming there was random search); there was, apparently, a high degree of mutual parasitoid interference ( $m$  large). In fact,

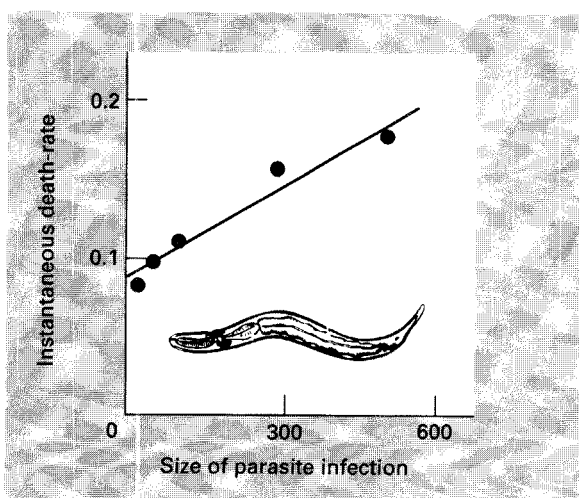


Fig. 5.29 The relationship between parasite death-rate and parasite density within individual hosts for chickens infected with the fowl nematode *Ascaridia lineata* (Ackert *et al.*, 1931). (After Anderson & May, 1978.)

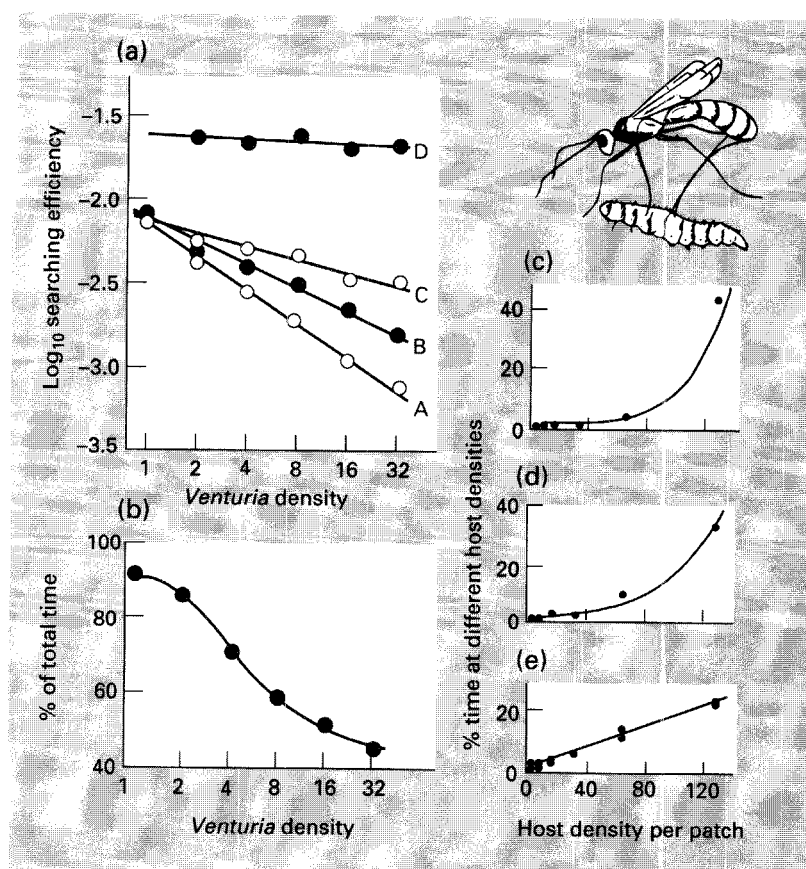


Fig. 5.30 (a) Relationships between searching efficiency and density of searching *Venturia canescens*; (b) relationship between (i) the proportion of time spent searching and *Venturia* density; and (ii) the percentage of time spent at different host densities with (c) one parasitoid, (d) two parasitoids, and (e) four, eight, 16 and 32 parasitoids. (After Hassell, 1978.) For further discussion, see text.

continuous observation showed *explicitly* that the time spent by parasitoids on host containers did decrease with increasing parasitoid density (Fig. 5.30b). In other words, mutual interference caused parasitoids to leave host patches, and thus spend less time searching. The true searching time, then, is not 24 hours, but the proportion of 24 hours indicated by Fig. 5.30b; and taking this into account increases the apparent searching efficiency and yields line B in Fig. 5.30a. Yet there is clearly some interference remaining after these effects have been removed.

A partial explanation of this is provided by the existence of an additional aspect of behavioural interference. Observation showed that parasitoid-parasitoid encounters often led not to departure from a patch, but simply to an interruption of probing (lasting about 1 min). This, too, can be used to reduce the 'true' searching time appropriately, because the

number of such encounters was observed and noted; and recalculating the apparent attacking efficiency this time yields line C in Fig. 5.30a.

Lines A–C have negative slopes (i.e. coefficients of interference) of 0.67, 0.45 and 0.27, respectively. Thus, 33% of the total interference  $[(0.67 - 0.45) / 0.67] \times 100$  is accounted for by parasitoids leaving host patches, and a further 27% by parasitoids simply interrupting their searching. However, this leaves 40% of the total unaccounted for by actual mutual interference. The preceding argument (Free *et al.*, 1977) would suggest that this is pseudo-interference, and the aggregative behaviour shown in Fig. 5.30c–e certainly supports this. Much more persuasive, however, is line D in Fig. 5.30a. This has been obtained by abandoning the assumption of random search, and using instead the observed data on search pattern from Fig. 5.30c–e. The slope,  $-0.03$ , indicates that there is no longer

any significant amount of interference. The interference of line C, in other words, was purely a consequence of the aggregative behaviour. It was, indeed, pseudo-interference.

Perhaps the initial conclusion to be drawn from this work is that, in the absence of the detailed observational data, it would have been impossible to partition the total interference of line A into mutual interference and pseudo-interference. This is not, however, as disappointing a conclusion as it might at first appear. In any natural situation, mutual interference (if it exists at all) is bound to increase with increased aggregation, since aggregation (by definition) leads to a higher probability of encounter. Yet the general effect of mutual interference will be to drive predators from dense aggregates (where encounters are most frequent). This will tend to reduce the level of aggregation, and ultimately reduce the mutual interference itself. There is, in short, a complex and dynamic interaction—which it might be extremely difficult to disentangle—between aggregation (leading to pseudo-interference) and behavioural interference; and it may, therefore, be convenient to encapsulate the effects of both in a single parameter: the coefficient of interference. Plots like the ones in Fig. 5.28 and line A in Fig. 5.30a, in other words, are able to capture the combined, density-dependent, stabilizing effects of aggregative behaviour and mutual predator interference; and there will be many natural situations in which one or both of these effects are extremely significant. Both effects, of course, represent strategies adopted by the predators to increase their own fitness.

### 5.11 Optimal foraging

One further conclusion that can be drawn from this discussion, however, is that the movement of predators between patches is itself worthy of detailed study whether this movement is a consequence of interference, or of patch depletion, or is even a means of patch assessment. Such study would be closely related to investigations of diet width among predators (section 5.3), and of the way in which predators distribute their effort amongst patches (section 5.7), because all three are concerned with the ways in which predators

tend to maximize their 'profits'. They can be bracketed together as studies of 'optimal foraging'. This is a subject which is reviewed in some detail by Stephens and Krebs (1986), but we can underline the importance of optimal foraging between patches by means of the following example.

Cook and Cockrell (1978) fed individual, fourth-instar mosquito larvae to adult water-boatmen, *Notonecta glauca*, and as Fig. 5.31a shows, the rate at which nutrients were extracted from a single prey item declined sharply with time. This occurred not because the water-boatmen were satiated, but because the food became increasingly difficult for them to extract. Without bending the rules too much, we can treat each prey item as a 'patch'. From this viewpoint we can see that the profitability of patches to water-boatmen declined rapidly the longer they stayed 'in' them. We can also see that to maximize their profits they would, at some time, have to leave depleted patches and find new, highly profitable ones, i.e. they would have to drop the old prey and catch a new one. Yet this in itself is a costly process: the predators take in no food while they are expending energy searching for, capturing and subduing (i.e. handling) the next prey item. Obviously, if they are to forage optimally, the water-boatmen must maximize their profits when they set such costs against the eventual gain from the new patch, and the longer the handling time the greater these costs will be. We would, therefore, expect optimally foraging predators to spend relatively long periods at a patch (where the rate of profit, even if low, is at least positive) when the handling time is high; and this is precisely the result obtained by Cook and Cockrell (Fig. 5.31b). The water-boatmen's feeding times served to increase their profits (Fig. 5.31c(i)). Prolonged stays (Fig. 5.31c(ii)) or repeated changes of patch (Fig. 5.31c(iii)) would clearly have been less profitable.

It must not, of course, be imagined that the water-boatmen consciously weigh up pros and cons and act accordingly. Rather, it is natural selection that has favoured individuals that adopt a strategy appropriate for foraging in a patchy environment with marked patch depletion. Nor must it be imagined that animals always adopt the strategy which actually maximizes

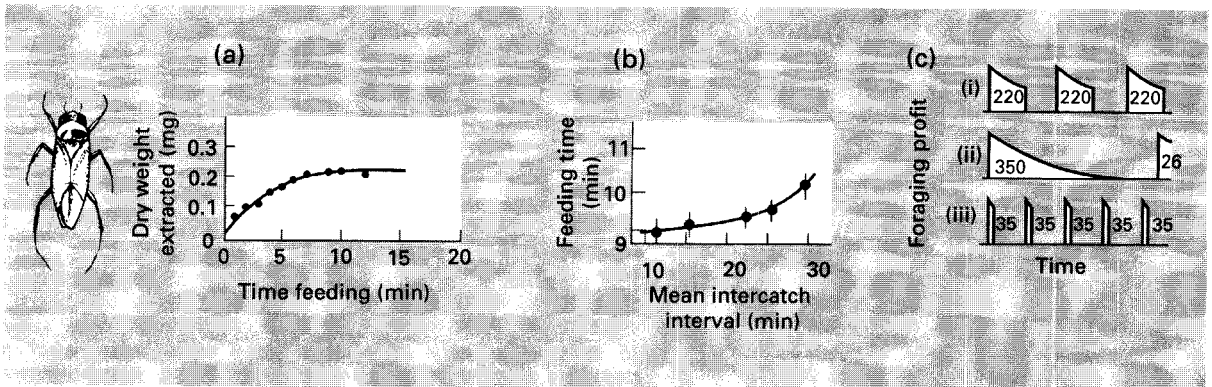


Fig. 5.31 (a) The cumulative dry weight of food extracted from an individual mosquito larva by *Notonecta* as a function of time spent feeding: as time increases, diminishing returns set in. (b) The relationship between feeding time ( $\pm$  SE) and handling time (intercatch interval).

(After Cook & Cockrell, 1978.) (c) The foraging profit of (i) an optimal forager (660 arbitrary units), compared to one with a long stay-time (ii) (376 units) and one with a short stay-time (iii) (175 units).

their foraging profits. As Comins and Hassell (1979) point out, animals must spend (i.e. 'waste') time sampling and learning about their environment; and the strategies they adopt will be influenced not only by foraging itself, but also by predator avoidance, and so on. Nevertheless, we can expect natural selection to exert evolutionary pressures *towards* an optimal foraging strategy; and the recognition of optimal foraging is bound to play an increasingly crucial role in our understanding of predator-prey interactions. Interestingly, Comins and Hassell (1979) suggested, from an analysis of models, that although optimal foraging has important consequences for predator fitness, its effects on predator-prey dynamics are rather similar to those resulting from a much simpler, fixed pattern of aggregation.

## 5.12 Résumé

Our view of the 'simplest, abstracted, two-species predator-prey system' is, by now, somewhat less naive than it was. We have seen that intraspecific competition amongst prey, 'type 3' functional responses, aggregated distributions of ill-effects (and, as special cases, spatial and temporal refuges), mutual interference amongst predators, and the increase in host immunological response with increased parasite

burden all tend to have a stabilizing influence on the interaction; while time-lags, the increased effects of multiple infections in parasites, the existence of 'maintenance thresholds' and 'type 1' and 'type 2' functional responses all tend to have a destabilizing influence. We have also seen that predators and prey exert a greater influence on the dynamics of one another's populations the more specific (less polyphagous) the predator is; that some prey have relatively little fitness to lose by their death; that the quality as well as the quantity of food can exert important influences on predator populations; and that, in many respects, predators *tend* to forage optimally.

Nevertheless, having examined these components we remain essentially ignorant of their relative importance, and of the patterns of abundance that we might expect them to give rise to, either alone or in combination. In order to go some way towards dispelling this ignorance, we turn, once again, to mathematical models.

## 5.13 Mathematical models

Of the models that we might consider, Lotka (1925) and Volterra (1926) constructed a classical, simple, continuous-time predator-prey model, which Rosenzweig and MacArthur (1963) developed further in

graphical form: Caughley and Lawton (1981) reviewed models of plant-herbivore systems; and Crofton (1971), Anderson and May (1978) and May and Anderson (1978) constructed models of the host-parasite interaction (reviewed by Anderson, 1981). However, because of the range of factors which they explicitly and successfully incorporate, we shall concentrate here on difference equation models of host-parasitoid systems (cf. section 3.2). These are described in much greater detail by Hassell (1978). Then, in section 5.13.3, we shall turn briefly to a model of grazing systems (Noy-Meir, 1975). The conclusions that we are able to draw throughout will throw important light on predator-prey interactions generally.

### 5.13.1 Host-parasitoid models

We begin by describing a very simple model, which can be used as a basis for further developments (Nicholson, 1933; Nicholson & Bailey, 1935). Let  $H_t$  be the number of hosts, and  $P_t$  the number of parasitoids (in generation  $t$ ):  $r$  is the intrinsic rate of natural increase of the host, and  $c$  is the conversion rate of hosts into parasitoids, i.e. the mean number of parasitoids emerging from each host. If  $H_a$  is the number of hosts actually attacked by parasitoids (in generation  $t$ ), then, clearly:

$$\begin{aligned} H_{t+1} &= e^r(H_t - H_a) \\ P_{t+1} &= cH_a \end{aligned} \quad (5.1)$$

In other words, ignoring intraspecific competition, the hosts that are not attacked reproduce, and those that are attacked yield not hosts but parasitoids. For simplicity we shall assume that each host can support only one parasitoid ( $c = 1$ ). Thus, the number of hosts attacked in one generation defines the number of parasitoids produced in the next ( $P_{t+1} = H_a$ ).

To derive a simple formulation for  $H_a$  we proceed as follows. Let  $E_t$  be the number of host-parasitoid encounters (or interactions) in generation  $t$ . Then if  $A$  is the proportion of the hosts encountered by any one parasitoid:

$$E_t = AH_tP_t$$

and

$$\frac{E_t}{H_t} = AP_t \quad (5.2)$$

( $A$  can, alternatively, be thought of as the parasitoid's searching efficiency; or the probability that a given parasitoid will encounter a given host; or, indeed, the 'area of discovery' of the parasitoid, within which it encounters all hosts.) Remember that we are dealing with parasitoids. This means that a single host can be encountered several times, but for the most part only the first encounter leads to successful parasitization; predators, by contrast, would physically remove their prey, and thus prevent re-encounters.

If encounters occur in an essentially random fashion, then the proportions of hosts encountered zero, one, two, three or more times are given by the successive terms in the appropriate 'Poisson distribution' (described in any basic textbook on statistics). The proportion *not* encountered at all,  $p_0$ , is given by:

$$p_0 = \exp\left(-\frac{E_t}{H_t}\right), \quad (5.3)$$

where  $\exp(-E_t/H_t)$  is another way of writing  $e^{-E_t/H_t}$ . Thus the proportion that *is* encountered (one or more times) is  $1 - p_0$ , and the *number* encountered (or attacked) is:

$$H_a = H_t(1 - p_0) = H_t\left\{1 - \exp\left(-\frac{E_t}{H_t}\right)\right\}$$

or

$$H_a = H_t\{1 - \exp(-AP_t)\} \quad (5.4)$$

And substituting this expression for  $H_a$  into equation 5.1 gives us:

$$\begin{aligned} H_{t+1} &= H_t \exp(r - AP_t) \\ P_{t+1} &= H_t \{1 - \exp(-AP_t)\}. \end{aligned} \quad (5.5)$$

This is the Nicholson-Bailey model of the host-parasitoid interaction. Its simplicity rests on two assumptions:

- 1 that parasitoid numbers are determined solely by the rate of random encounters with hosts; and
- 2 that host numbers would grow exponentially but for the removal of individuals by random encounter with parasitoids.

As Hassell (1978) makes clear, an equilibrium combination of these two populations is a *possibility*, but even the slightest disturbance from this equilibrium leads to divergent oscillations (Fig. 5.32). Thus, our simple model, although it produces coupled oscillations, is highly unstable. Nevertheless, it is clearly a formal restatement of the naive expectation expressed in section 5.1: when a single predator and a single prey interact in the simplest imaginable way, coupled oscillations are the result.

Since most observed patterns of abundance are considerably more stable than those produced by the Nicholson–Bailey model, we must be particularly interested in modifications to it which enhance stability. The most obvious modification we can make is to replace the exponential growth of hosts with density-dependent growth resulting from intraspecific competition (section 5.5). Following Beddington *et al.* (1975), this is done by incorporating a term like the one used in the logistic equation (section 3.3), giving

$$\begin{aligned} H_{t+1} &= H_t \exp \left\{ r \left( 1 - \frac{H_t}{K} \right) - AP_t \right\} \\ P_{t+1} &= H_t \{ 1 - \exp(-AP_t) \} \end{aligned} \quad (5.6)$$

where  $K$  is the carrying-capacity of the host popula-

tion in the absence of parasitoids. Figure 5.33 illustrates the patterns of abundance resulting from this revised model in terms of  $r$  and a new parameter,  $q$  ( $= H^*/K$ ) where  $H^*$  is the equilibrium size of the host population in the presence of parasitoids. For a given value of  $r$  and  $K$ ,  $q$  depends solely on the parasitoids' efficiency,  $A$ . When  $A$  is low,  $q$  is almost 1 ( $H^* = K$ ), but at higher efficiencies  $q$  approaches zero ( $H^* \ll K$ ).

It is clear from Fig. 5.33 that intraspecific competition amongst hosts can lead to a range of abundance patterns. Moreover, intraspecific competition is obviously a potentially important stabilizing factor in host–parasitoid systems. This is particularly so for low and moderate values of  $r$ , and high and moderate values of  $q$ ; but even with low values of  $q$  (high parasitoid efficiency), the fluctuations are not altogether unlike those observed in natural populations. Note, however, that with high reproductive-rates and low parasitoid efficiencies we return to the chaotic behaviour characteristic of the single-species populations in section 3.4.1.

The next modification we can make to the Nicholson–Bailey model is to consider explicitly the parasitoids' functional response to host density (section 5.7). In the present context, this is described by

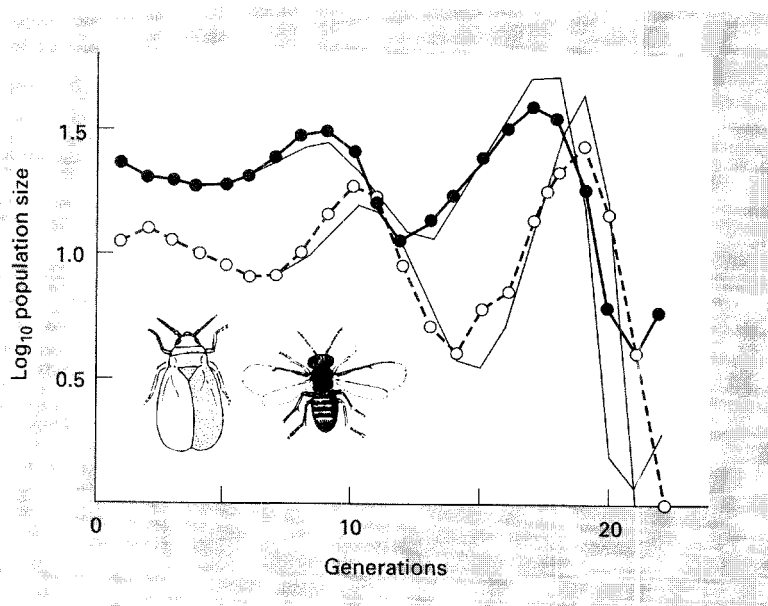


Fig. 5.32 Population fluctuations from an interaction between the greenhouse whitefly *Trialeurodes vaporariorum* (●) and its chalcid parasitoid *Encarsia formosa* (○). The thin lines show the estimated outcome from a Nicholson–Bailey model (Burnett, 1958). (After Hassell, 1978.)

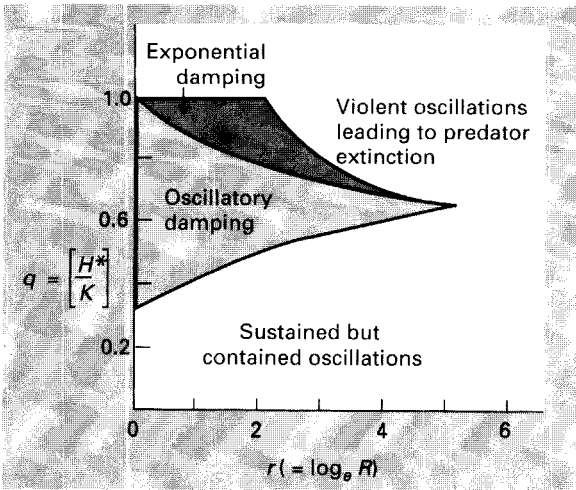


Fig. 5.33 Stability boundaries for the parasitoid–host model with intraspecific host competition, as in equation 5.6. (After Beddington *et al.*, 1975.) For further discussion, see text.

the relationship between  $H_a/P_t$  (the mean number of hosts attacked per parasitoid) and  $H_t$ ; i.e. the relationship between the number of hosts attacked by a constant number of parasitoids ( $H_a$  with  $P_t$  constant) and  $H_t$ . Until now we have been assuming that this relationship is linear (equation 5.4):

$$H_a = H_t \{1 - \exp(-AP_t)\}.$$

In other words, it is implicit in the Nicholson–Bailey model that the ‘predation’-rate of the parasitoids continues to rise indefinitely with increasing host density, i.e. handling time is zero. This is clearly at variance with the data examined in section 5.7, and is, in any case, impossible. Obviously it is important to replace this linear relationship with the types 2 and 3 functional responses which are actually observed.

Dealing first with the type 2 response, we saw in section 5.7.1 that the essential feature underlying it is the existence of a finite ‘handling time’. Thus, we shall let  $T$  be the total amount of time available to each parasitoid,  $T_h$  the time it takes to deal with *each* host (handling time),  $T_s$  the total amount of time available to each parasitoid for host seeking, and  $a$  the parasitoids’ instantaneous rate of search (or attack-rate, see section 5.7). Then, by definition:

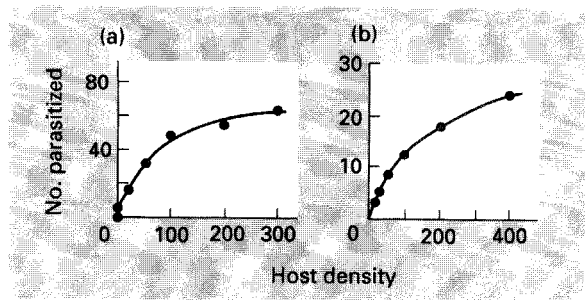


Fig. 5.34 Type 2 functional responses generated by equations 5.7. (a) *Nasonia vitripennis* parasitizing *Musca domestica* pupae (DeBach & Smith, 1941)  $a = 0.027$ ;  $T_h = 0.52$ . (b) *Dahlbominus fuscipennis* parasitizing *Neodiprion sertifer* cocoons (Burnett, 1956;  $a = 0.252$ ;  $T_h = 0.037$ . (After Hassell, 1978.)

$$\Lambda = aT_s,$$

So that the total number of hosts handled in generation  $t$  by each parasitoid is now  $aT_s H_t$ . If we consider that ‘total available search time’ is equal to ‘total time’ minus ‘total handling time’, then:

$$T_s = T - T_h aT_s H_t,$$

which, by rearrangement, gives:

$$T_s = \frac{T}{1 + aT_h H_t},$$

so that:

$$\Lambda = \frac{aT}{1 + aT_h H_t}.$$

Substituting this into equations 5.4 and 5.5 gives:

$$H_a = H_t \left\{ 1 - \exp \left( \frac{-aTP_t}{1 + aT_h H_t} \right) \right\} \quad (5.7)$$

$$H_{t+1} = H_t \exp \left( r - \frac{aTP_t}{1 + aT_h H_t} \right)$$

$$P_{t+1} = H_t \left\{ 1 - \exp \left( \frac{-aTP_t}{1 + aT_h H_t} \right) \right\} \quad (5.8)$$

As Fig. 5.34 shows, equation 5.7 generates a type 2 functional response, in which the maximum possible number of hosts attacked is determined (as expected) by  $T_h/T$ , and the rate of approach to this asymptote is determined by  $a$  (the instantaneous search-rate). Equation 5.8, therefore, represent the Nicholson–



Bailey model with a type 2 functional response incorporated into it. Their dynamic properties were examined by Hassell and May (1973) and, as expected, the inverse density-dependence makes this model less stable than the Nicholson-Bailey (recovered from this model when  $T_h = 0$ ). However, increased instability is relatively slight as long as  $T_h/T \ll 1$ , and we can see in Table 5.8 (Hassell, 1978) that this is, indeed, generally the case. This model indicates, therefore, that the destabilizing tendencies of type 2 functional responses are unlikely to be of major importance in nature.

In order to model the type 3 functional response, we shall follow the pragmatic approach of Hassell (1978), and assume first that only the instantaneous search-rate,  $a$ , varies with host density, and second that it does so in the simplest way compatible with the data examined in section 5.7.3, namely

$$a = \frac{xH_t}{1 + yH_t},$$

where  $x$  and  $y$  are constants. Substituting this into equations 5.7 and 5.8 (and rearranging) gives us:

$$H_a = H_t \left\{ 1 - \exp \left( \frac{-xTH_t P_t}{1 + yH_t + xT_h H_t^2} \right) \right\} \quad (5.9)$$

$$H_{t+1} = H_t \exp \left( r - \frac{xTH_t P_t}{1 + yH_t + xT_h H_t^2} \right) \quad (5.10a)$$

$$P_{t+1} = H_t \left\{ 1 - \exp \left( \frac{-xTH_t P_t}{1 + yH_t + xT_h H_t^2} \right) \right\}. \quad (5.10b)$$

Equation 5.9 generates a type 3 functional response, and equations 5.10a and b are, therefore, the Nicholson-Bailey model with a type 3 response incorporated into it.

We have already noted (in section 5.7.4) that the density-dependent aspect of this response is likely to have an essentially stabilizing effect, but, as with the type 2 response, examination of the appropriate model allows us to make an interesting qualification to this informal conclusion. In particular, Hassell and Comins (1978) found that in the situation we have been dealing with—one host and one parasitoid coupled together in a *discrete-generation* model—a type 3 response *alone* is incapable of stabilizing the interaction. Conversely, there are at least two alternative situations in which it becomes a much more potent stabilizing force. The first is when the time delay of discrete generations is removed and replaced by the instantaneous reaction of continuous breeding (Murdoch & Oaten, 1975). The second is when the parasitoid is polyphagous, and the type 3 response is a result of parasitoid 'switching'. Hassell and Comins (1978) believe that this behaviour would essentially allow the parasitoid to maintain itself at a constant density, so that:

$$P_t = P_{t+1} = P^*.$$

And if this equation is merged with equation 5.10a, then the patterns of abundance are as summarized in Fig. 5.35.

Table 5.8 Estimated values of handling time  $T_h$  from equation 5.7 for a selection of parasitoids. The values of  $T_h/T$  are based on conservative estimates of longevity. (After Hassell, 1978.)

Parasitoid species	Host	Handling time $T_h$ (hours)	$T_h/T$	References
<i>Venturia canescens</i>	<i>Ephestia cautella</i>	0.007	< 0.0001	Hassell & Rogers, 1972
<i>Chelonus texanus</i>	<i>Ephestia kuehniella</i>	0.12	< 0.001	Ulyyett, 1949a
<i>Dahlbominus fuscipennis</i>	<i>Neodiprion lecontei</i>	0.24	< 0.003	Burnett, 1958
<i>Pleolophus basizonus</i>	<i>Neodiprion sertifer</i>	0.72	< 0.02	Griffiths, 1969
<i>Dahlbominus fuscipennis</i>	<i>Neodiprion sertifer</i>	0.96	< 0.01	Burnett 1954
<i>Cryptus inornatus</i>	<i>Loxostege sticticalis</i>	1.44	< 0.02	Ulyyett, 1949b

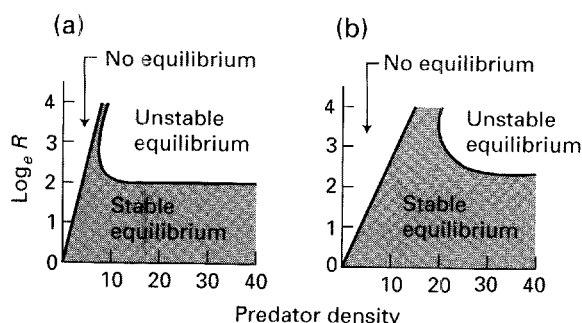


Fig. 5.35 Stability boundaries for the parasitoid–host model with constant parasitoid density (parasitoid switching) and the host as described in equation 5.10a. (a)  $y = 0$ ; (b)  $y = 2\sqrt{(xT_h)}$ . (After Hassell & Comins, 1978.)

Overall, therefore, these models make it clear that the apparently simple consequences of the different ‘predator’ functional responses are subject to significant qualifications.

We turn now to the important question of heterogeneity (section 5.8), and consider first the special, extreme case of a host ‘refuge’. If there is a *constant proportion* refuge such that only a proportion of the hosts,  $\gamma$ , are available to the parasitoids, then equations 5.5 can be replaced simply by:

$$\begin{aligned} H_{t+1} &= (1 - \gamma)H_t e^r + \gamma H_t \exp(r - AP_t) \\ P_{t+1} &= \gamma H_t \{1 - \exp(-AP_t)\}. \end{aligned} \quad (5.11)$$

Conversely, if there is a *constant number* refuge in which  $H_0$  hosts are always protected, the appropriate modification is:

$$\begin{aligned} H_{t+1} &= H_0 e^r + (H_t - H_0) \exp\{r - AP_t\} \\ P_{t+1} &= (H_t - H_0) (1 - \exp\{-AP_t\}). \end{aligned} \quad (5.12)$$

The results of these modifications are summarized in Fig. 5.36 (following Hassell & May, 1973). It is clear that, while both modifications have a stabilizing effect on the interaction, the constant *number* refuge is by far the more potent of the two. This is no doubt due to the density-dependent effect of having a greater proportion of the host population protected as host density decreases.

By contrast, a very much more general approach to heterogeneity has been taken by May (1978a). He set aside the precise nature of host and parasitoid distri-

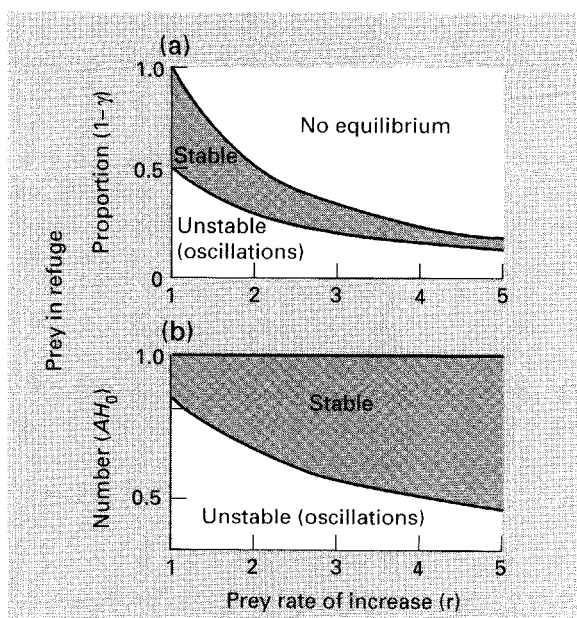


Fig. 5.36 The effects of refuges on stability: (a) a constant proportion refuge (equations 5.11), and (b) a constant number refuge (equation 5.12). (After Hassell & May, 1973.)

butions and efforts, and argued simply that the distribution of host–parasitoid *encounters* was not random but aggregated. In particular, he assumed (with some justification—see May, 1978a) that this distribution could be described by the simplest and most general of the appropriate statistical models, the negative binomial. In this case, the proportion of hosts not encountered at all is given by:

$$p_0 = \left[1 + \frac{AP_t}{k}\right]^{-k}$$

where  $k$  is a measure of the degree of aggregation: maximal aggregation at  $k = 0$ , minimal aggregation at  $k = \infty$  (recovery of the Nicholson–Bailey model). The appropriate modification of  $p_0$  in equations 5.6 gives us a model that incorporates both aggregated encounters and intraspecific competition amongst hosts:

$$\begin{aligned} H_{t+1} &= H_t \exp\left\{r\left(1 - \frac{H_t}{K}\right)\right\} \left[1 + \frac{AP_t}{k}\right]^{-k} \\ P_{t+1} &= H_t \left(1 - \left[1 + \frac{AP_t}{k}\right]^{-k}\right). \end{aligned} \quad (5.13)$$

The patterns of abundance generated by this model are summarized in Fig. 5.37, from which it is clear that the already moderately stable system described by equation 5.6 is given a marked boost in stability by the incorporation of significant levels of aggregation ( $k \leq 1$ ). Of particular importance is the existence of stable systems with very low values of  $q$ . Of the stabilizing factors so far considered, encounter aggregation (i.e. heterogeneity) is obviously the most potent.

We consider next a topic that was established in section 5.9 as being closely connected with the aggregation of encounters: mutual parasitoid interference. Following Hassell and Varley (1969), we shall adopt a simple, empirical approach and derive a form for the searching efficiency,  $A$ , which conforms to the log-log plots of Fig. 5.28, i.e.

$$A = QP_t^{-m}$$

where  $\log Q$  and  $-m$  are the intercept and slope of the plots, and, in particular,  $m$  is the 'coefficient of interference'. Note that, because this relationship is empirical, it serves to describe not only interference proper but pseudo-interference as well. The relation-

ship, therefore, incorporates mutual parasitoid interference and aggregation.

The appropriate model is clearly:

$$\begin{aligned} H_{t+1} &= H_t \exp(r - QP_t^{1-m}) \\ P_{t+1} &= H_t \{1 - \exp(-QP_t^{1-m})\} \end{aligned} \quad (5.14)$$

and the patterns of abundance resulting from these equations are illustrated in Fig. 5.38. Not surprisingly, since aggregation of encounters is being incorporated, 'total interference' is shown to be an extremely potent stabilizing force.

### 5.13.2 Heterogeneity in host-parasitoid interactions

We have already seen in the previous section that the tendency for parasitoids to aggregate in areas of high host density can be a powerful stabilizing force in host-parasitoid systems. The models of that section (Hassell & May, 1973, 1974; Murdoch & Oaten, 1975; May, 1978a) showed that the stability observed was the result of directly density-dependent mortality. However, it is now clear that other types of mortality contribute to stability in host-parasitoid interactions. Spatial variation in parasitism that is *independent* of host density and that which shows *inverse* density-dependent mortality can also contribute in a signifi-

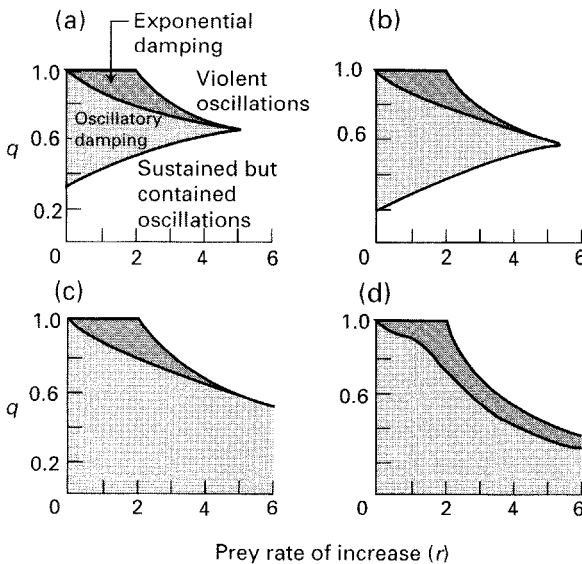


Fig. 5.37 Stability boundaries for the parasitoid-host model with parasitoid aggregations as in equations 5.13: (a)  $k = \infty$ ; (b)  $k = 2$ ; (c)  $k = 1$ ; (d)  $k = 0$ . (After Hassell, 1978.) (See Fig. 5.33.)

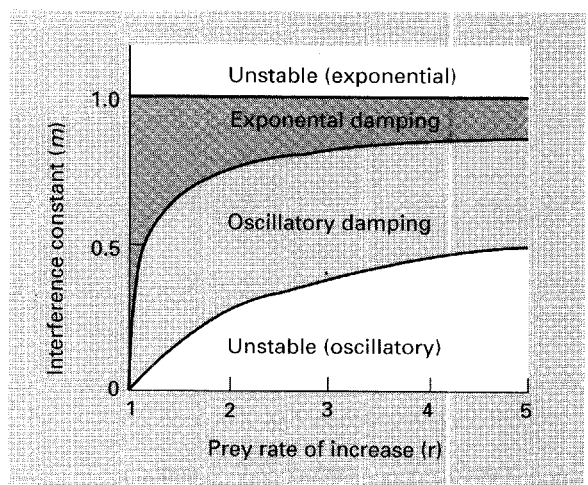
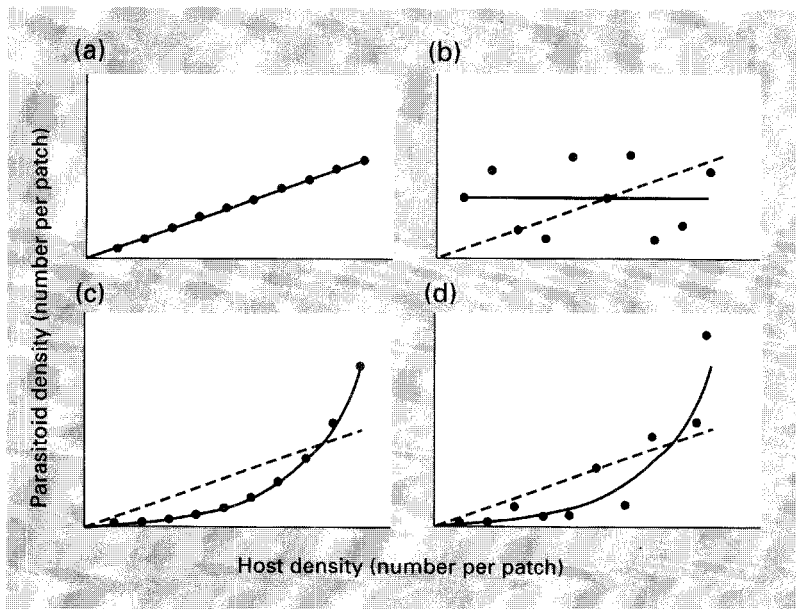


Fig. 5.38 Stability boundaries for the parasitoid-host model with mutual interference as in equations 5.14. (After Hassell & May, 1973.)

cant way to stability (Chesson & Murdoch, 1986; Pacala *et al.*, 1990; Hassell *et al.*, 1991).

The concept that underlies how these different density-related mortalities can stabilize host-parasitoid interactions is the 'relative risk of parasitism' for a host individual (Chesson & Murdoch, 1986) and is illustrated in Fig. 5.39. This 'risk' refers to a heterogeneous distribution across hosts of the probability of encounters with parasitoids — all hosts are not equally likely to be parasitized (except in the unusual circumstance shown in Fig. 5.39a). There are essentially two ways in which hosts have a high risk of being parasitized. The first is if parasitoids aggregate in patches independently of host density (Fig. 5.39b). In

such instances, those hosts that occur in patches into which parasitoids have aggregated are more likely to be parasitized than those in patches which have low parasitoid numbers. The second is if they occur in patches of high host density, into which parasitoids aggregate in response to host density. In particular if the relationship between parasitoid density and host density between patches is an accelerating one (i.e. a power function), then hosts in the highest host density patches are more likely to be parasitized than in any lower host density patches (Fig. 5.39c). In each of these two scenarios the converse is, of course, also important. In the first example, patches in which there are many hosts but few parasitoids will be



**Fig. 5.39** Four possible relationships between parasitoid and host density. In (a) there is no aggregation of risk, with the same ratio of parasitoids to hosts in each patch. (b) This is a host-density-independent (HDI) model in which parasitoids are aggregated, but not in relation to host density. There is a high risk of parasitism when parasitoid numbers in a given patch lie above the dashed line ( $\equiv$  'no aggregation of risk line' of part (a)) and correspondingly a low risk when parasitoid numbers are below this line. The solid line in (c) represents a host-density-dependent (HDD) model in which parasitoids are once again aggregated, but this time in response to host density. Once again there is a high risk of parasitism when parasitoid numbers in a given

patch lie above the dashed line and correspondingly a low risk of parasitism when parasitoid numbers are below this line. In (d) a data set typical of those reported in field studies is shown. The solid line of best fit to the data is identical to that shown in the HDD model of (c). Parasitoids are again seen to be aggregating in patches of high host density, but in this example the match between parasitoid density and host density is not perfect.  $CV^2$  is calculated as follows: divide parasitoid numbers by host numbers in each patch to give 'risk of parasitism'; calculate the mean 'risk of parasitism' and its variance; divide the variance by the square of the mean.

refuges for the hosts. In the second example, low host density patches effectively become refuges from parasitism.

We imagine that parasitoids frequently aggregate in patches of high host density, but that the matching of host and parasitoid density is far from perfect (Fig. 5.39d). The two scenarios we have presented represent opposite ends of a continuum. Hassell *et al.* (1991) refer to models that are closest to the first scenario as host-density-independent heterogeneity models (HDI) and those that resemble the second as host-density-dependent heterogeneity models (HDD).

The aggregation of risk of parasitism can be measured by the ratio of the standard deviation of the risk of parasitism per host divided by the mean risk of parasitism, or the coefficient of variation (CV). For some discrete time models of host–parasitoid interactions the criterion for stability of the host–parasitoid interaction is that  $CV^2 > 1$  (Pacala *et al.*, 1990; Hassell *et al.*, 1991). Stability through heterogeneity in the probability of encounters is achieved through strengthening density-dependencies, specifically through pseudo-interference (see section 5.10 and Taylor, 1993). Pseudo-interference refers to reduction in parasitoid efficiency resulting from an increasing number of host–parasitoid encounters involving previously parasitized hosts. By increasing this pseudo-interference, aggregation of risk makes host mortality less dependent on parasitoid density and conversely reduces per capita parasitoid recruitment. The result is that parasitoids have a lesser impact on host density and oscillations in parasitoid density are damped (Taylor, 1993). Stability is thus promoted.

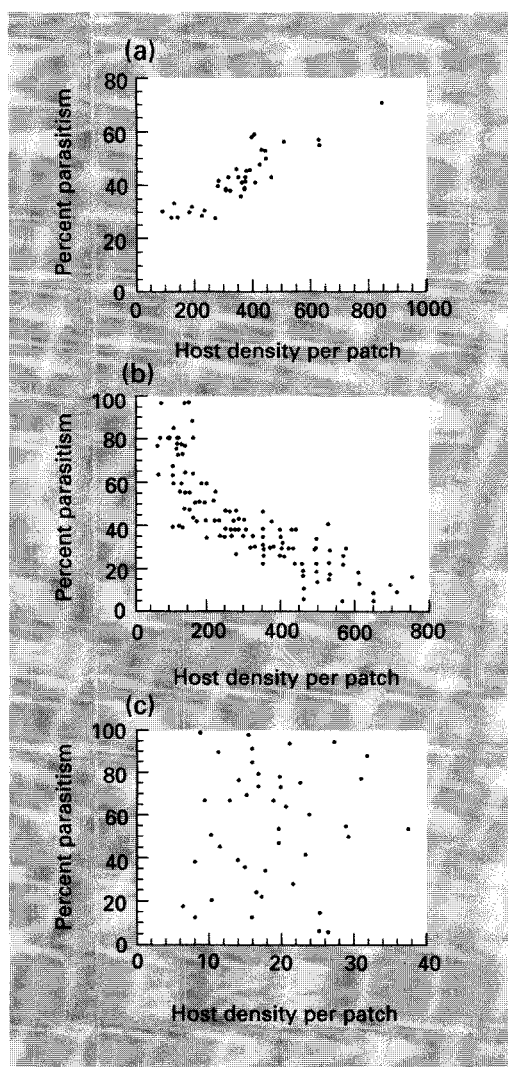
By partitioning  $CV^2$  into components, it is possible to show that both density-dependent and density-independent patterns of parasitoid distribution contribute to stability in the same way. What is particularly interesting and surprising about this approach is the finding that density-independent heterogeneity can contribute so much to stability. Hassell *et al.* (1991) and Pacala and Hassell (1991) examined the contribution of HDI and HDD to population stability by applying the  $CV^2$  criterion to five host–parasitoid models which made different assumptions about host and parasitoid distributions. In each case

the  $CV^2$  rule was a good indicator of stability. However, the models examined did all make some assumptions—namely (i) that interactions between parasitoid and host were coupled and synchronized; (ii) that there were discrete host and parasitoid generations; (iii) that exploitation of hosts within a patch was random; and (iv) that there was no interference between parasitoids or competition between hosts.

A criterion such as the  $CV^2$  rule is only of any use to a population ecologist if the parameters necessary to calculate  $CV^2$  can be estimated from field data. The rule,  $CV^2 > 1$  is in terms of the distribution of searching parasitoids, but such data are rarely available from natural populations. Data from host–parasitoid interactions are usually in the form of a relationship between percentage parasitism and host density per patch; some examples are shown in Fig. 5.40. Pacala and Hassell (1991) explain how the parameters necessary to calculate  $CV^2$  can be estimated from typical field data.

Hassell and Pacala (1990) analysed 65 field studies that reported per cent parasitism and local host density per patch and from which estimates of  $CV^2$  could be made. In 18 of these 65 studies  $CV^2 > 1$  which suggests that the heterogeneity present, if it was repeated from generation to generation, would be sufficient to stabilize the interaction between the host and parasitoid populations. In 14 of the 18 examples in which  $CV^2 > 1$ , the component of heterogeneity that was independent of host density was greater than that which was dependent on host density, indicating that HDI heterogeneity contributes most to the total heterogeneity, and therefore most towards stability, more often than HDD heterogeneity. This finding goes against the conventional wisdom that stability can only be promoted by density-dependent factors alone. We shall return to this topic in Chapter 6.

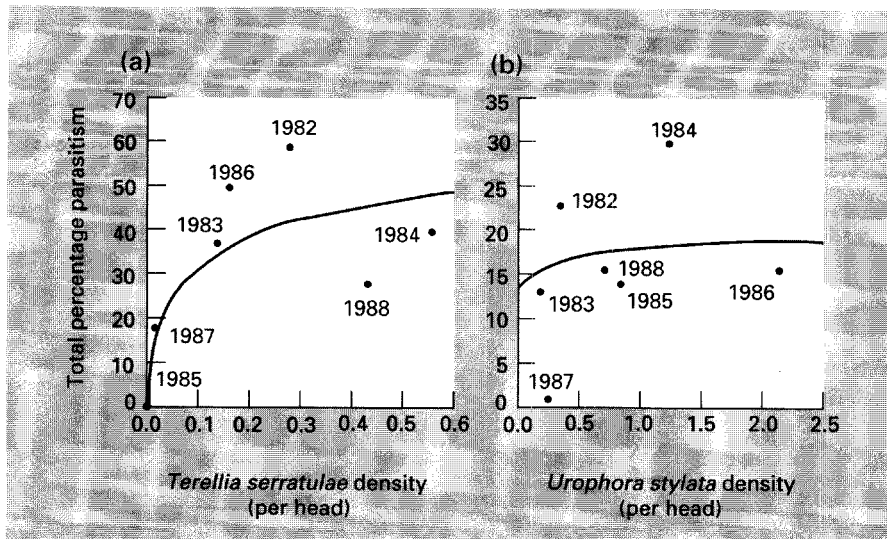
The spatial distributions of two tephritid flies (*Urophora stylata* (F.) and *Terellia serratulae* L.) attacking thistle flower heads and the levels of parasitism from six associated parasitoids were examined over a 7-year period in the field by Redfern *et al.* (1992). These data provide a rare opportunity to seek both temporal density-dependent parasitism between average parasitoid density and host density per generation



**Fig. 5.40** Three examples from field studies of different patterns of parasitism from patch to patch; (a) direct density-dependent parasitism of the scale insect *Fiorinia externa* by the eulophid parasitoid *Aspidiotiphagus citrinus* on the lower crown of 30 hemlock trees (McClure, 1977); (b) inverse density-dependent parasitism of gypsy moth *Lymantria dispar* eggs by the encyrtid parasitoid *Ooencyrtus kuwanai* (Brown & Cameron, 1979); (c) density-independent parasitism of gall midge *Rhopalomyia californica* by the Torymid parasitoid *Torymus baccaridis* (Ehler, 1987). (After Hassell *et al.*, 1991.)

as well as any spatial patterns that may be operating within the same system, and to assess their relative contributions to stability using the approach outlined above. Figure 5.41 shows the relationship between total percentage parasitism and the density of the tephritid hosts per flower head. There is significant density-dependent mortality between total parasitism of *T. serratulae* and host density per year (Fig. 5.41a), which is the result of the combined parasitism of the two main parasitoids, *Pteromalus elevatus* and *Tetrastichus cirsi*. The comparable analysis for *Urophora stylata* shows no such relationship (Fig. 5.41b). The spatial analysis of parasitism is summarized in Fig. 5.42, which shows the temporal variation in  $CV^2$  and its HDI and HDD components for the total parasitism of each host species.  $CV^2 > 1$  in 5 of the 6 years in which parasitism was observed for *U. stylata*. In each case this stability is brought about largely as a result of HDI components of heterogeneity (Fig. 5.42a).  $CV^2 > 1$  in only 1 of 5 years in which parasitism was observed for *Terellia serratulae*, but once again HDI was responsible rather than HDD (Fig. 5.42b). The results of this study indicate how parasitism may be regulating two tephritid species. There appears to be conventional temporal density-dependence contributing to the stability of the interaction of *T. serratulae* and its parasitoids with little evidence for stabilizing heterogeneity. In contrast, there is no evidence of temporal density-dependence in this relatively short run of data for *Urophora stylata*, but there is considerable potentially stabilizing heterogeneity, which may have a considerable impact on the dynamics of the host.

How general is the  $CV^2 > 1$  rule? Future work is likely to show that it has been useful in focusing attention on the role of aggregation of risk in promoting stability, rather than being absolutely right. While the rule holds for a range of non-overlapping generation discrete time host-parasitoid models, of the type described by equation 5.1, it is clear that there is a range of factors not incorporated into the models of Hassell *et al.* (1991) which can alter the degree of aggregation of risk needed for stability. Some of these factors are common in nature. For example when the functional response of the parasitoid is type 1 (as

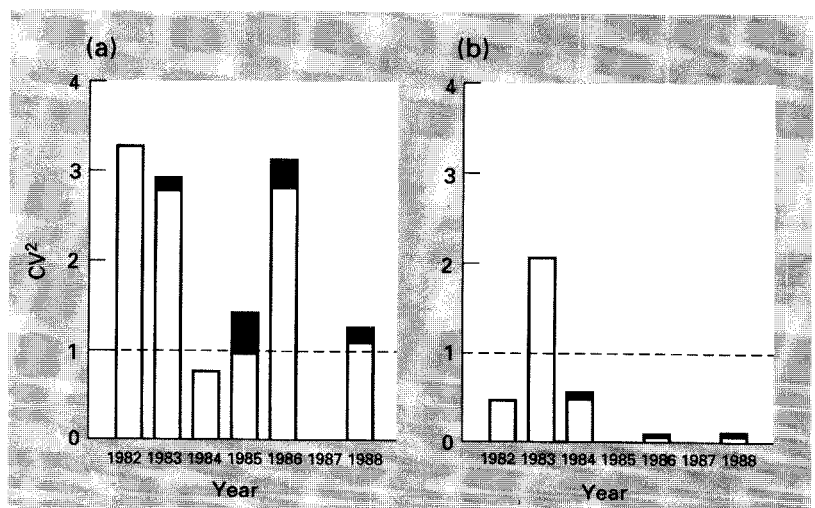


**Fig. 5.41** Total parasitism from generation to generation in relation to the average density of tephritid hosts per flower head for the period 1982–88. Fitted line given by equation  $y = a + b \log_{10} x$ . (a) *Terellia serratulae*:  $a = 56.07$  (SE 10.45);  $b = 9.90$  (SE 9.90);  $r^2 = 0.75$ ,  $P < 0.05$ ; (b) *Urophora stylata*:  $a = 17.26$  (SE 3.46);  $b = 11.70$  (SE 10.49);  $r^2 = 0.44$ ,  $P > 0.05$ . (After Redfern *et al.*, 1992.)

assumed in the models examined above), density-dependent parasitism is always stabilizing. However, parasitoid functional responses are more typically of type 2. In such cases initial increases in density-

dependent aggregation from zero are destabilizing, and only large amounts of density-dependent parasitoid aggregation are stabilizing—when handling time reduces parasitoid efficiency in high host density patches (Ives, 1992a,b).

The most obvious violation of the assumptions of the  $CV^2 > 1$  rule in its application to date is that many of the field studies analysed, including the one described above, involve more than one parasitoid–host interaction and two or more competing host species. Others include several parasitoid species whose effect some-



**Fig. 5.42** Values of  $CV^2$  for the period 1982–88 for total parasitism of (a) *Urophora stylata*, and (b) *Terellia serratulae*. The proportional contribution of the host-density-dependent (dark shading) and host-density-independent (light shading) components to the total  $CV^2$  is also illustrated. (After Redfern *et al.*, 1992.)

times was lumped in total parasitism. The effects of additional species vary. When two specialized parasitoids share a host species greater aggregation is required for stability than with a single parasitoid. However, a generalist parasitoid whose parasitism rate is positively correlated with host density provides additional stability (Taylor, 1993).

The models considered in this section have been in discrete time with non-overlapping generations. The role of aggregation by parasitoids in a heterogeneous environment in continuous time models with overlapping generations is controversial. Murdoch and Stewart-Oaten (1989) found that aggregation independent of host density did not affect stability and that aggregation to patches of high host density was typically destabilizing. Ives (1992a,b) concluded, and we can only agree with him, that there is such a wealth of dynamic complexity in continuous-time models that it may be impossible to apply the conclusions from any model to a real parasitoid–host system without detailed observations and experiments on the hosts and parasitoids in question.

### 5.13.3 A model of grazing systems

We turn now to a model of grazing systems developed by Noy-Meir (1975). It is typical of a range of models, all of which essentially incorporate the ‘Allee effect’ (section 2.6); and all such models indicate that predators and their prey (in this case grazers and their food plants) can coexist at *more than one stable equilibrium*

(see May, 1977 for a review).

We have already seen (in section 5.5.1) that plant populations, with the individuals growing as multiply branched units, may not necessarily exhibit a simple pattern of population growth. In particular, we argued that the rate of vegetative growth may be conveniently expressed in terms of photosynthetic assimilation, the *net* assimilation rate being the rate of biomass growth having accounted for respiratory losses. Figure 5.43 demonstrates that if the rate of growth in biomass is plotted against the leaf area index (the ratio of total leaf area to horizontal ground beneath the canopy), then there is an intermediate, optimum index which maximizes growth-rate—a result of the shifting balance between photosynthesis and respiration as biomass and *shading* increase. Not surprisingly, since total biomass and leaf area index are so closely associated, there is also a humped, curved relationship between growth-rate and biomass. The actual shape of such curves (e.g. Fig. 5.44) will depend on the interaction of many factors (see Blackman, 1968 for a review), but in all cases an optimum biomass will exist, yielding a maximum growth-rate.

Conversely, the removal of vegetation biomass occurs as a result of grazing, and we have seen that the rate of herbivore consumption depends on a variety of factors. In broad terms, however, consumption-rate is likely to follow the saturation curve of a ‘type 2’ or, more rarely, a ‘type 3’ functional response (section 5.7). Of course, the *total* rate of herbivore consumption will increase with herbivore density. This will result in

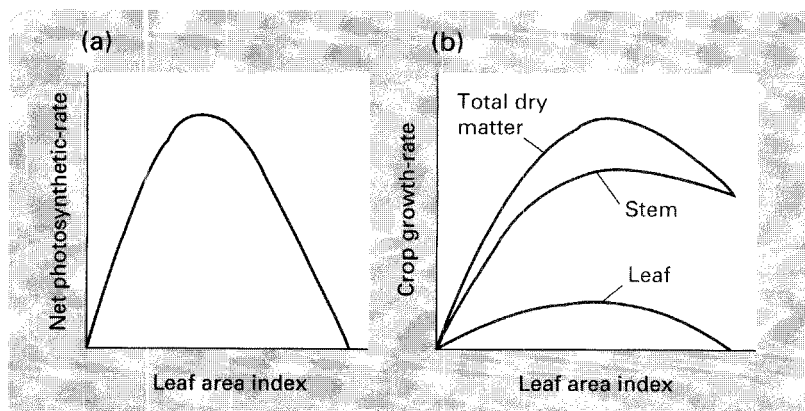


Fig. 5.43 (a) Idealized relationship between crop growth-rate and leaf area index. (b) Actual relationship found in subterranean clover by Davidson and Donald (1958). (After Donald, 1961.)



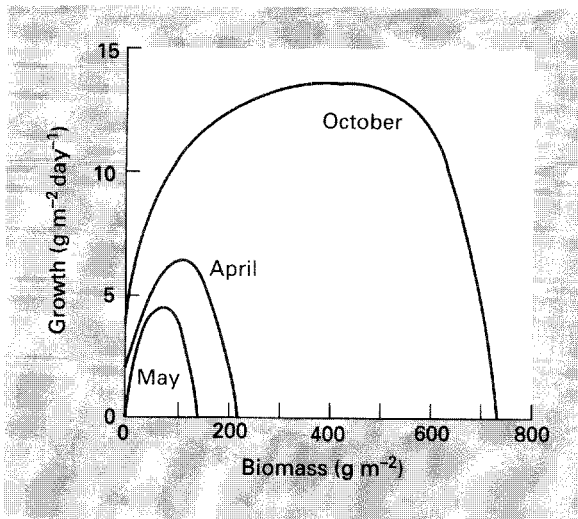


Fig. 5.44 Plant growth in New Zealand ryegrass-clover pastures as a function of biomass (Brougham, 1955, 1956). (After Noy-Meir, 1975.)

a family of curves, all of similar shape, but with the height of the maximal, saturation consumption-rate itself increasing with herbivore density (see, for instance, Fig. 5.45a).

We now have two families of curves; and they can be used to model the outcome of grazing by superimposing them on one another, because the difference between the rates of growth and consumption gives the *net* change in the growth-rate of vegetation biomass. In Figs 5.45a, 5.46a, 5.47a and 5.48a, the growth- and consumption-rates are plotted against biomass for four different sets of conditions. These allow the net growth-rates to be inferred for various combinations of herbivore density and biomass, and this information is summarized in the corresponding Figs 5.45b, 5.46b, 5.47b and 5.48b. These illustrate the positions of the biomass zero isoclines, separating circumstances of positive and negative biomass growth.

The simplest grazing model is shown in Fig. 5.45. For each type 2 herbivore consumption curve (Fig. 5.45a), biomass increases below point A (because

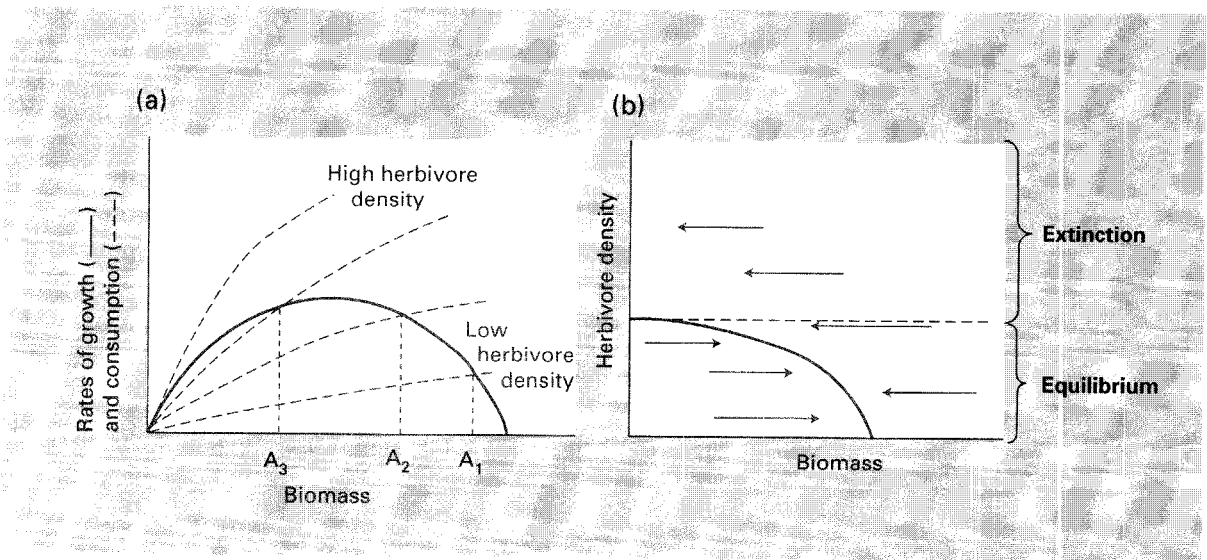


Fig. 5.45 (a) Rates of plant growth and herbivore consumption (at a range of herbivore densities) plotted against plant biomass.  $A_1$ ,  $A_2$  and  $A_3$  are stable equilibria at which growth- and consumption-rates are equal. (b) The isocline dividing combinations of plant biomass and

herbivore density which lead to biomass increase (arrows left to right) from combinations which lead to biomass decrease (arrows right to left). (After Noy-Meir, 1975.) For further discussion, see text.

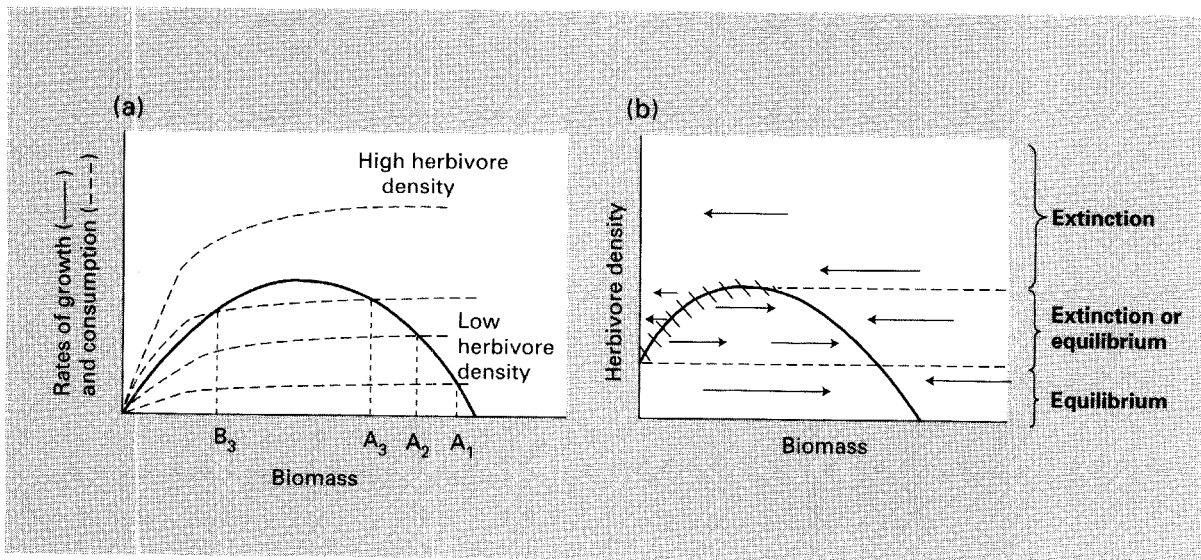


Fig. 5.46 Similar to Fig. 5.45 except that in (a), as a result of altered consumption-rate curves, there is an unstable equilibrium at intermediate herbivore densities,  $B_3$ ; and in (b) there is a shaded area close to the isocline, indicating combinations of plant biomass and herbivore density at which minor changes in either could alter the outcome from stable equilibrium to plant decline and ultimate extinction, or vice versa. For further discussion, see text.

growth exceeds consumption), but decreases above point A (consumption exceeds growth). Each point A is, therefore, a stable equilibrium. As herbivore densities increase, however, (and *total* consumption increases) the level of stable biomass reduces (shown by the shape of the isocline in Fig. 5.45b), and at herbivore densities exceeding some critical value, consumption is greater than growth for all levels of biomass and the plant population is driven to extinction; this is obviously not unreasonable.

A slightly more complex situation, in which the consumption curve reaches saturation more suddenly, is shown in Fig. 5.46. The outcome is unchanged at low herbivore densities (equilibrium) and at high herbivore densities (extinction); but at intermediate densities, the consumption-rate curve crosses the growth-rate curve twice (points A and B). As before, biomass decreases above point A (because consumption exceeds growth), but this is now also true *below*

point B; while between points A and B, growth exceeds consumption, and biomass increases. Point A is, therefore, still an essentially stable equilibrium, but point B is an unstable *turning point*. A biomass slightly less than B will decrease to extinction, driven by overconsumption; a biomass slightly greater than B will increase to the stable equilibrium at point A. As Fig. 5.46b makes clear, then, there is an intermediate range of herbivore densities at which *either* equilibrium *or* extinction is possible, and small changes in herbivore density or vegetation biomass occurring close to the isocline in this region (hatched in Fig. 5.46b) can obviously have crucial effects on the outcome of the interaction.

In Figs 5.47 and 5.48 two even more complex situations are illustrated, but in general terms the outcomes are the same in both. Figure 5.47 represents a plant population that maintains a *reserve* of material which is not accessible to grazers (underground storage organs, for example, or plant parts which are inedible). The origin of the growth-rate curve is, therefore, displaced to the left of the origin of the consumption-rate curve. Figure 5.48 represents a herbivore population exhibiting a 'type 3' functional response. In both cases, the outcome is unchanged at low herbivore densities; there is a single, stable equilibrium (point A).

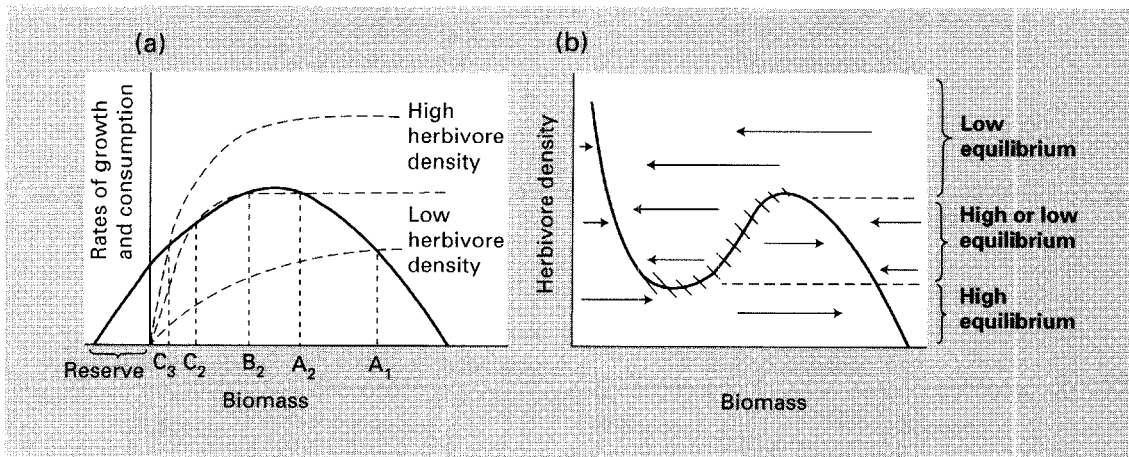


Fig. 5.47 Similar to Fig. 5.46 except that there is a 'reserve' of ungrazable plant biomass. As a consequence there are in (a) low biomass stable equilibria at high and intermediate herbivore densities ( $C_2$  and  $C_3$ ). The shaded area in (b), therefore, indicates combinations of plant biomass and

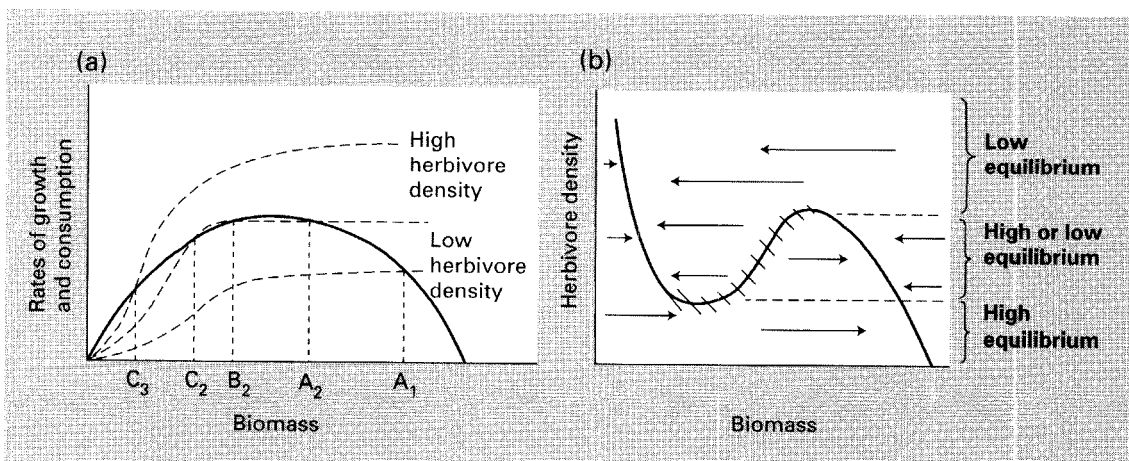
herbivore density at which minor changes in either could alter the outcome from low biomass stable equilibrium to high biomass stable equilibrium, and vice versa. For further discussion, see text.

At high herbivore densities, however, the plant population is no longer driven to extinction (ungrazable reserves and type 3 responses stabilize the interaction). Instead there is a point,  $C_3$ , at which the two curves cross, such that growth exceeds consumption below  $C_3$ , while consumption exceeds growth

above it. These high density cases are, therefore, *also* characterized by a single, stable equilibrium. However, while the low herbivore density equilibria were maintained at a high biomass by the self-regulatory properties of the plants, these high herbivore density equilibria are maintained at a *low* biomass by either the ungrazable reserves of the plants or the functional response of the herbivore.

Fig. 5.48 Similar to Figs 5.45 and 5.46 except that the herbivores exhibit a sigmoidal, type 3 functional response. In other respects the figure is like Fig. 5.47. For further discussion, see text.

Moreover, at intermediate herbivore densities in Figs 5.47a and 5.48a, the consumption curve crosses



the growth curve at *three* points ( $A_2$ ,  $B_2$  and  $C_2$ ). As before, point A is a high biomass stable equilibrium, point C is a low biomass stable equilibrium, and point B is an unstable turning point. Populations in the region of point B, therefore, might increase to point A or decrease to point C, depending on very slight, perhaps random changes in circumstances. These plant-herbivore systems have *alternative stable states*; and a small change in the size of either the plant or the grazer population in the hatched regions of Figs 5.47b or 5.48b can shift the system rapidly from one stable state to the other. The crucial point, therefore, is that systems with ungrazable reserves or type 3 functional responses may undergo sudden drastic changes in population levels, which are nonetheless grounded in the regulatory dynamics of the interaction.

It is difficult to evaluate this model's predictions critically, because much of the data on grazing is not amenable to this form of analysis. Yet the available evidence for Australian pastures certainly suggests that combinations of observed growth and consumption curves may well lead to situations with alternative stable states (Fig. 5.49); and as Noy-Meir (1975) has argued, the predictions of the model are borne out by the experiences of agronomists and range managers. In particular, one practice often recommended in the

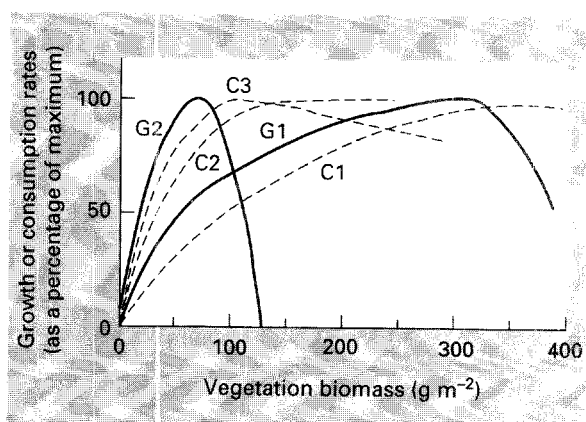


Fig. 5.49 Experimentally obtained curves of growth,  $G$  (ryegrass and subterranean clover) and consumption,  $C$  (by sheep), standardized to maximum rates of 100%. (After Noy-Meir, 1975.)

management of grazing stock is to delay the start of grazing until a minimum of vegetation growth has been exceeded. It is clear that for a given herbivore density this will tend to prevent extinction in Fig. 5.46, while in Figs 5.47 and 5.48 it will favour a high biomass equilibrium, where the plant growth-rate and thus the food available to the grazers will also be high.

Finally, it must be admitted that this 'one plant/one grazer' model is an unrealistic abstraction of the real, multi-species world. Nevertheless, it provides a simple and effective framework for the comparison and analysis of plant-herbivore dynamics, and also indicates the complex, indeterminate, multi-equilibrial behaviour of predator-prey systems generally.

#### 5.14 'Patterns of abundance' reconsidered

This chapter began, after some preliminary definitions, with an outline survey of the patterns of abundance associated with predation; and, since 'predation' was defined so inclusively, this was effectively a survey of abundance patterns generally. Now, having examined many of the components of 'predatory' interactions, we ought to be in a position to reconsider these patterns. But we must remember that no 'predator-prey system' exists in a vacuum: both species will also be interacting with further species in the same or different trophic levels. Thus, Anderson (1979) considered that parasites probably often play a *complementary* role in the regulation of host populations, increasing their susceptibility to predation (though evidence for this is mainly anecdotal). Similarly, Whittaker (1979) concluded that quite moderate levels of grazing will often produce a severe effect on a target plant when (and because) they are combined with (otherwise ineffective) interspecific plant competition. Lawton and McNeill (1979) concluded that plant-feeding insects stood between the 'devil' of their natural enemies, and the 'deep blue sea' of '... food that, at best, is often nutritionally inadequate and, at worst, is simply poisonous'. Finally, Keith (1963) suggested because of hare cycles on a lynx-free island that the (supposedly) classical snowshoe hare/Canada lynx predator-prey oscillations (see Fig. 5.1a) are

actually a result, at least in part, of the hare's interaction with its food. It is clear, in short, that to truly understand the patterns of abundance exhibited by different types of species, we must consider, synthetically, all of their interactions.

Nevertheless, it is apparent from this chapter that we have at our disposal a wealth of *plausible* explanations for the patterns of abundance that occur. Individually, each of the components can give rise to a whole range of abundance patterns, and in combination their potentialities are virtually limitless. What we lack, regrettably, is the sort of detailed field information that would allow us to decide which explanations apply in which particular situations. We are forced, simply, to conclude—and this is especially apparent in the mathematical models—that observed patterns of abundance reflect a state of dynamic tension between the various stabilizing and destabilizing aspects of the interactions.

Beyond this, we can point to food aggregation, and the aggregative responses of consumers to this aggregation, as probably the single most important factor stabilizing predator–prey interactions. Indeed, Beddington *et al.* (1978) noted that the biological control of insect pests is characterized by a persistent, strong reduction in the pest population following the introduction of a natural enemy (i.e. stability at low  $q$ ); and they suggested, from the analysis of mathematical models, that the mechanism which is most likely to account for this is the differential exploitation of pest patches in a spatially heterogeneous environment. (Even more important than this is the fact that they were able to marshal several field examples in support of this suggestion.) In brief, it appears that aggregation is of very general significance in maintaining prey populations at stable, low densities.

A further insight, stemming from mathematical models, is that predator–prey systems can exist in more than one stable state. Indeed the model in the previous section is only one of a range that possess such properties (see May, 1977, 1979 for reviews), and this range covers predator–prey, host–parasitoid, plant–herbivore and host–parasite interactions. We therefore have a ready explanation for parasite epidemics, pest outbreaks, and sudden, drastic alterations in density generally.

Finally, *in general*, we have seen that very similar principles apply to all those interactions included within the blanket term 'predation'; and in all cases, there has been considerable progress in understanding the details underlying the relationships. Overall, however, it must be admitted that while there is nothing in the observed patterns of abundance that should surprise us by being essentially inexplicable, we are rarely in a position to apply specific explanations to particular sets of field data.

## 5.15 Harvesting

In this section, we are concerned with examining the dynamics of populations that regularly suffer loss of individuals as a consequence of the deliberate attentions of mankind, through cropping or harvesting. In all predator–prey interactions the predator will profit by maximizing the crop taken while ensuring that the prey does not become extinct; and we have already seen, in this chapter, that in natural populations the survival of a certain number of prey individuals will tend to be ensured as a by-product of certain features of the interaction. In the instances involving man as the harvester, however, the problem of *conscious* harvest optimization remains, i.e. the problem of ensuring neither *over-exploitation* (hastening extinction) nor *under-exploitation* (cropping less than the prey population can sustain). It is with this in mind that many ecologists have devoted considerable attention to the manner in which plant and animal populations can be exploited for the benefit of mankind.

### 5.15.1 Characteristics of harvested populations

From the outset we can see, from common sense alone, that the first, immediate consequence of harvesting is to reduce the size of the population, and this, in turn, will generally affect the life expectancy and fecundity of the survivors in the harvested population. Nicholson (1954a), for instance, cultured Australian sheep blowflies (*Lucilia cuprina*) under conditions that restricted adult food supplies but provided larvae with a food excess (ensuring very little larval mortality). His

**Table 5.9** Effects produced in populations of the blowfly, *Lucilla cuprina*, by the destruction of different constant percentages of emerging adults. (After Nicholson, 1954a.)

Exploitation-rate of emerging adults (%)	Pupae produced per day (a)	Adults emerged pre day (b)	Mean adult population (c)	Mean birth rate (per individual per day) (a/c)	Natural adult deaths per day	Adults destroyed per day (d)	Accessions of adults per day (e = b - d)	Mean adult life span (days) (c/e)
0	624	573	2520	0.25	573	0	573	4.4
50	782	712	2335	0.33	356	356	356	6.6
75	948	878	1588	0.60	220	658	220	7.2
90	1361	1260	878	1.55	125	1134	126	7.0

results (Table 5.9) show that, whilst the adult population declined with increasing exploitation, both pupal production and adult emergence *increased*, resulting in an overall increase in the 'birth'-rate. Coincident with this rise, moreover, was a decrease in the rate of natural adult death, and this led to extension of the mean adult life span. The reduction in population size resulting from the act of harvesting, therefore, brought about two changes: (i) increased fecundity of surviving adults; and (ii) reduced adult mortality; and, indeed, we might have expected this from our knowledge of the effects of intraspecific competition (Chapter 2). Reduction in population density in a resource-limited environment tends to benefit the individual survivors.

The act of harvesting also has an important effect on the *rate of regrowth* of the population. This can easily be seen by considering a population undergoing density-dependent regulation and following a logistic growth curve (Fig. 5.50). At a point in time,  $t_2$  (when the population has reached a size,  $N_2$ ) we remove some individuals from the population, i.e. we *crop* it. The population will continue to grow, but from the reduced size ( $H_1$ ) that it had already reached at time  $t_1$ . Clearly, the rate of growth of the population after harvesting (the slope of the curve) will depend on the time at which the harvesting occurred. If removal takes place early (Fig. 5.50a), then the rate of subsequent growth will be low, and indeed reduced by harvesting. If removal takes place late (Fig. 5.50c), then the rate of growth, though increased, will also be low. If, however, it takes place when the population is growing most rapidly (Fig. 5.50b), then the rate will be

high and largely unchanged by the removal. Moreover, the population size prior to harvest and the rate of subsequent regrowth are also related to the *size* of repeated harvests taken after a unit period of recovery (Figs 5.50 and 5.51). At low population sizes, successive harvests are small (Fig. 5.51a), but with increasing population size they increase steadily to a maximum and then decline; and as Fig. 5.51b shows, there is a parabolic relationship between harvest size and population size. There is, therefore, an *optimal* size at which a population can be maintained, which, on repeated harvesting, ensures a *maximum sustainable harvest*; and repeated harvesting at this size is also followed by the rapid recovery of the population because its rate of regrowth is maximal. Note that in the case of Nicholson's blowflies (see Table 5.9), harvest-size ('adults destroyed per day') continued to rise as the exploitation level increased and the mean population size decreased. There was also a consistent rise in the rate of regrowth (compounded from an increased number of 'adults emerged' and a decreased rate of 'natural adult death'). It seems, therefore, that these populations were towards the right-hand side of the appropriate parabola, where intraspecific competition was fairly intense. For the logistic equation itself, the optimum population size is in fact  $K/2$  (where  $K$  is the carrying-capacity) and we can show this mathematically by differential calculus. (Readers familiar with calculus will know that 'finding the maximum of a function' involves differentiating the appropriate equation—the logistic in this case—setting the derivative to zero, and solving for  $N$ .) The important biolo-

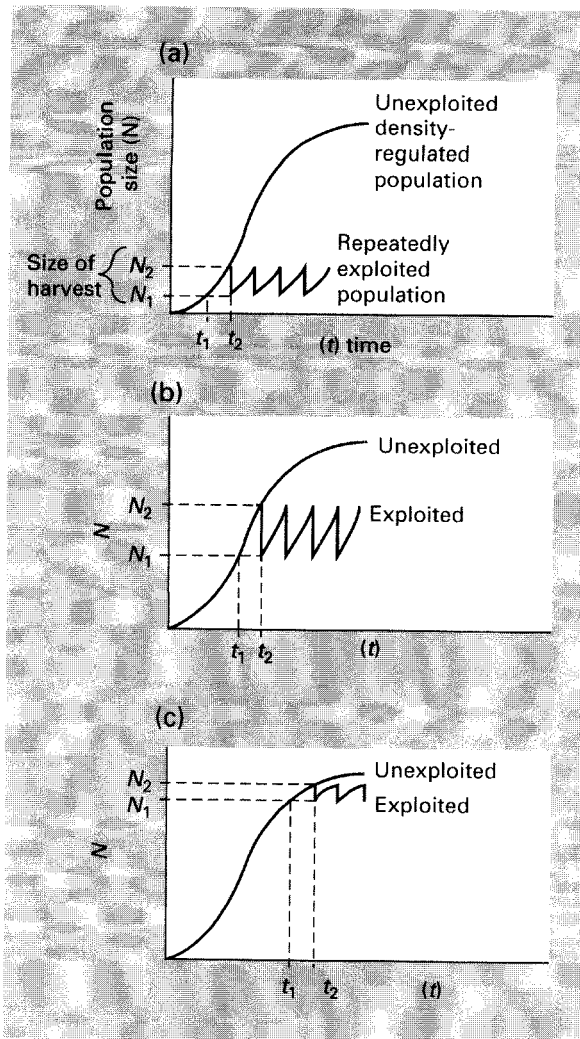


Fig. 5.50 The effects of harvesting at (a) early, (b) middle and (c) late stages of population growth with the population growing logistically. For further discussion, see text.

gical point to realize, however, is that the maximum sustainable harvest is not obtained from populations at the carrying-capacity,  $K$ , but from populations at lower, intermediate densities, where they are growing fastest. The exact shape of the *harvest parabola* depends on the growth function, and the harvest parabolas of different sigmoidal growth curves will vary accordingly. The 'logistic' parabola is symmetrical because the logistic curve itself is symmetrical.

Some justification for this type of model is provided by studies of harvested fish populations. Since it is impossible to estimate the sizes of oceanic fish population numerically, stock sizes (or total biomass) can be used instead. The equation describing the changes must be:

$$S_{\text{year } 2} = S_{\text{year } 1} + \text{Rec} + G - D - C$$

where  $S$  is stock size, and  $\text{Rec}$  is recruitment of stock,  $G$  growth,  $D$  loss by natural mortality and  $C$  stock caught by fishing. If stock size remains constant from one year to the next then:

$$\text{Rec} + G = D + C.$$

In other words, at *any* stock size, if the stock is in a *steady state*, then the gains from recruitment and growth will be exactly offset by the losses from natural mortality and fishing. So, if the stock is growing logistically, and we wish to *maintain steady-state conditions*, then we must exploit the stock according to the harvest parabola. Figure 5.52a shows the catch sizes of yellow fin tuna from 1934 to 1955 plotted against fishing intensity (a measure recorded by the fishing industry that may easily be related to stock size). Interestingly, the actual recorded catches do seem to lie on the estimated harvest parabola; and indeed the size of the catch from 1934 to 1950 was increased by 100 million pounds *without* destroying the fish population, and from 1948 onwards large catches *could* be sustained. A fairly similar situation is shown for a lobster fishery in Fig. 5.52b. It does appear, therefore, that at least some fisheries are regulated in a density-dependent and possibly even logistic fashion.

It would be gratifying to be able to claim that the management and conservation of all exploited fish populations are based on detailed knowledge and careful modelling. Yet, while substantial research in the fishing industry has deepened our understanding of the factors influencing the stability and yield of exploited populations (Beverton & Holt, 1957; Gulland, 1962), for three main reasons we are still unable to fully comprehend their dynamics. The first reason is a genuine ignorance of population dynamics: obtaining the data for long-lived species demands extensive and often expensive study over many seasons. The



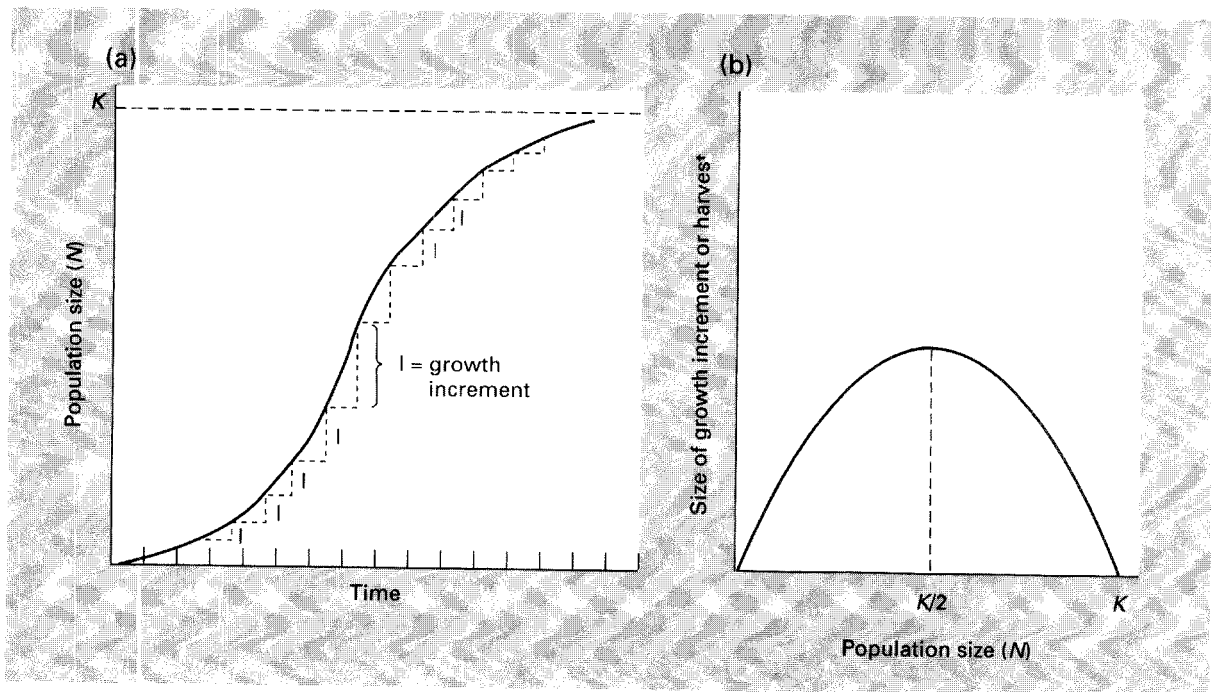


Fig. 5.51 (a) Growth increments in unit periods of time at different stages of growth of a population growing logistically. (b) The parabolic relationship between these increments (or, alternatively, the size of repeated harvests) and population size.

second reason is that many populations are structured, and we shall consider this problem presently. The third reason is environmental variability. The environment, particularly climate, frequently affects natural populations independently of density, and environmental fluctuations may, therefore, create considerable difficulty in the evaluation of the effects of harvesting on population size. This is illustrated by data on the Pacific sardine, *Sardinops caerulea*, off the coast of California, where the annual catch exhibits extreme fluctuations (Fig. 5.53a). There has been considerable controversy over the relationship between the population sizes of: (i) the 'spawning stock'; (ii) the mature breeding fish (2 years old and over); and (iii) the 2-year-old recruits; and although Murphy (1967) has established that the number of recruits is partly determined by the water temperature when the

fish were spawned (Fig. 5.53b), there are other environmental variables that play a highly significant role. The movements of ocean currents within the coastal nursery grounds, for instance, are often seasonally erratic, and young planktonic fish may be swept into the deep ocean where they are unlikely to survive. Temperature, currents and other factors, then, are all likely to blur any relationship between the size of the breeding population and the number of offspring born to it. However, Radovich (1962) has argued that the recruitment relationship is in fact curvilinear with a recognizable optimum. Thus, in Fig. 5.53c three curves have been drawn: II gives the best statistical fit to the data, while I and III have been drawn by inspection to encompass the variability observed. I represents the relationship we might expect when environmental factors combine to give the 'best' possible conditions, and III the relationship for the 'worst' conditions. The clear consequence of this underlying curvilinearity is that recruitment tends to be little affected by changes in spawning stock size near the optima, but is more drastically affected at the extremes. The utility of these curves stems from the



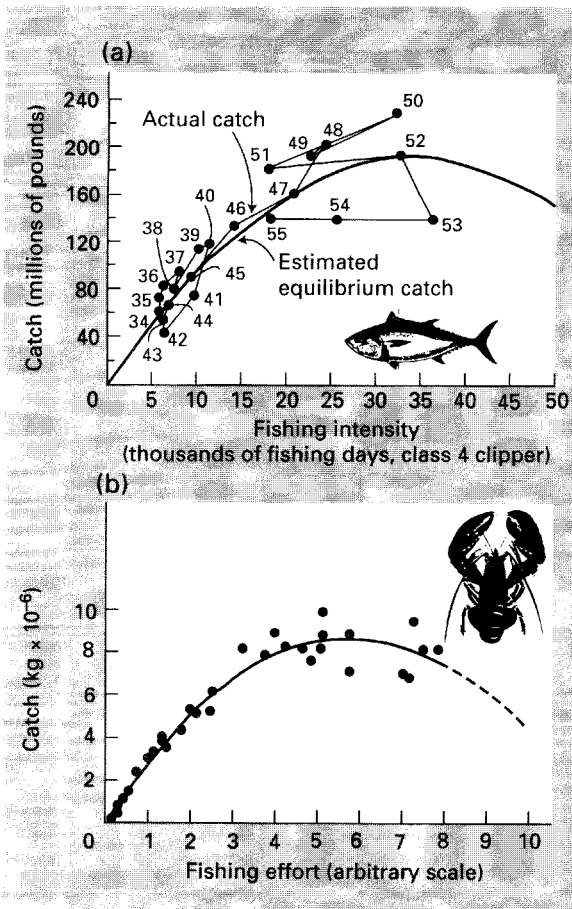
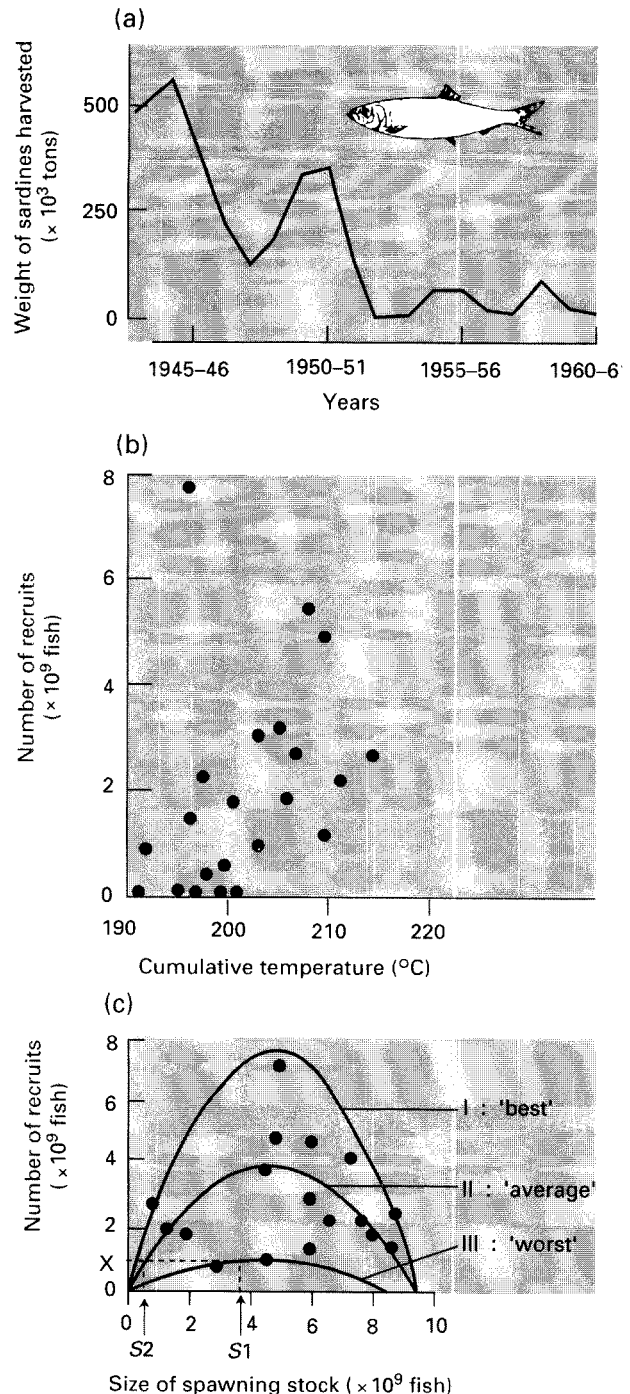


Fig. 5.52 (a) The relationship between fishing intensity and yield of yellow fin tuna in the eastern pacific between 1934 and 1955. The curved line is the estimated harvest parabola (Schaefer, 1957). (After Watt, 1968). (b) Similar relationship for the western rock lobster *Palinurus cygnus* (Hancock, 1979). (After Beddington, 1979.)

ability they give us to assess the levels of fishing that safeguard against extinction even under the poorest circumstances. If for instance we wish to ensure a consistent recruitment  $X$  (Fig. 5.53c), then the bare

Fig. 5.53 (a) The annual catch of the Californian sardine, and (b) the effect of sea temperature on the recruitment of the sardine (Watt, 1968). (c) The average parabola relating the number of recruits to the size of the spawning stock, together with the maximum and minimum parabolas (Radovich, 1962). For further discussion, see text. (After Usher, 1972.)



minimum of stock that must be left after harvesting under the 'average' conditions is  $S_2$ . The difference,  $S_1 - S_2$ , represents the additional stock that should not be harvested if we wish to guarantee recruitment when recruitment is lowest, in the 'poorest' environment. Overall, the problems of incorporating environmental variability into a predictive harvesting model are readily apparent (but see Iles, 1973 for a more sophisticated attempt to overcome these problems).

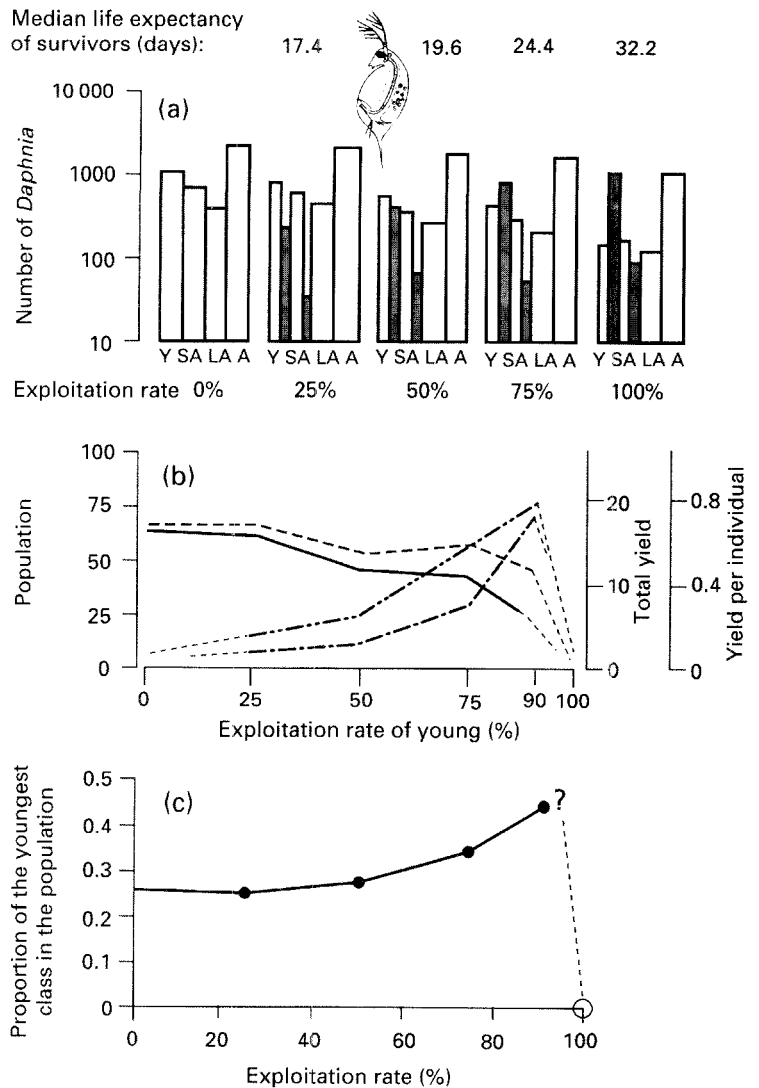
We are now in a position to review some of the consequences of harvesting. First, it is quite clear that populations can be systematically exploited with a consequent reduction in population size. It is also clear that harvests can be optimized (i.e. the size of repeated harvests maximized) by harvesting at some intermediate density where the population growth-rate is greatest. However, such harvesting is only sustainable at an exploitation-rate that allows sufficient time for the replacement of cropped individuals. This period of time will depend on the fecundity and generation time of the species in question. It is easy to imagine an intensity of harvesting (an exploitation-rate) in excess of the replacement-rate, such that the population declines to extinction ('stepping down' the curve in Fig. 5.51a). We can also conclude (from the *Lucilia* population, and from a consideration of intraspecific competition) that the fitness of survivors in a harvested population is often increased.

### 5.15.2 Harvesting in structured populations

In practice, many harvesting procedures deliberately select individuals to be cropped. In fishing, for instance, many nets permit small fry to escape so that large (and possibly older) individuals are captured. In other situations (seal culling for instance) small or young members are the principal object of the harvest. We must therefore consider the age and size composition of populations being exploited.

To investigate the properties of such structured populations in the field under particular harvesting regimes is an immensely arduous task, and, in consequence, many workers have utilized relatively simple laboratory systems. A good example is the work of Slobodkin and Richman (1956) using water fleas

(*Daphnia pulicaria*), which breed continuously throughout the year and possess a prodigious capability for population increase by virtue of the very large number of eggs they lay. They are also particularly convenient for harvesting studies because they have a short life span; and in their population structure we can recognize young, adolescent and adult forms. Figures 5.54a and 5.54b show the consequences of taking harvests every 4 days from *Daphnia* populations which were maintained with a constant supply of food at a constant temperature for about 9 months. Harvesting was aimed specifically at the smallest size-class which (apart from a few young adolescents) contained *Daphnia* which were less than 4 days old. The population structure in the absence of harvesting is shown in Fig. 5.54a, '0%': the numbers per class decline to a minimum at the large adolescent stage (L.A.), and the adult class is the most abundant (the data are presented on a logarithmic scale). Increasing the proportion of young fleas harvested had two main effects. The first was to reduce consistently the total population size (Fig. 5.54a & 5.54b). The second was to alter the population structure (Fig. 5.54a): as the harvesting of small *Daphnia* increased from 25 to 90% of their number, the discrepancy between young, small and large adolescent frequencies diminished. We may note in addition, however, that 90% exploitation did not push the population towards extinction, and indeed, there was a consistent rise in total yield as exploitation-rate increased (Fig. 5.54b). This occurred because the yield *per individual* rose quickly enough to more than compensate for the decline in population size (Fig. 5.54b); and this consistent rise in the fitness of survivors (cf. Nicholson's blowflies) was also reflected by a steady increase in life expectancy averaged over all size-classes (Fig. 5.54a). Such increases were associated, moreover, with a consistent rise in the proportion in the population of the exploited, youngest class prior to harvesting (Fig. 5.54c), i.e. a further indication of the changing population structure. This presumably occurred because exploitation reduced the numbers available to enter the older classes, and also reduced intraspecific competition, leading to an increased *per capita* production of the youngest class such that its *proportion* in the popula-



**Fig. 5.54** (a) The effect of harvesting on the size structure of a *Daphnia* population, where the size-classes are: Y, young; SA, small adolescent; LA, large adolescent; and A, adult. The shaded halves of the columns represent those removed and the open halves those left after harvesting. (b) The effect of harvesting on mean population size before harvest (---), mean population size after harvest (—), total yield (---) and yield per individual (---). (c) The effect of harvesting on the proportion of the youngest class in the total population (all Slobodkin & Richman, 1956). For further discussion, see text. (After Usher, 1974.)

tion increased. For the exploitation-rates examined here, these effects apparently more than compensated for the losses due to harvesting, in that there was a consistent increase in yield. Beyond some higher point, however, increases in productivity would be unable to compensate for reductions in numbers, and the population would decline to extinction. In the present case, this point is apparently between 90 and 100% exploitation.

Parenthetically, we should note that once we have accepted that populations are structured, it is impor-

tant to determine whether 'yield' should be measured in terms of number or biomass, since the two are not necessarily equivalent. Figure 5.55 (Usher *et al.*, 1971) illustrates this problem in populations of an invertebrate herbivore, the collembolan *Folsomia candida*. The populations were subjected to regular harvesting over all size-classes at rates of 0, 30 and 60% of the total population every 14 days, and the animals were always given excess food. Harvesting reduced the numerical size of the *Folsomia* populations far less than it reduced their biomass. Moreover, the crop

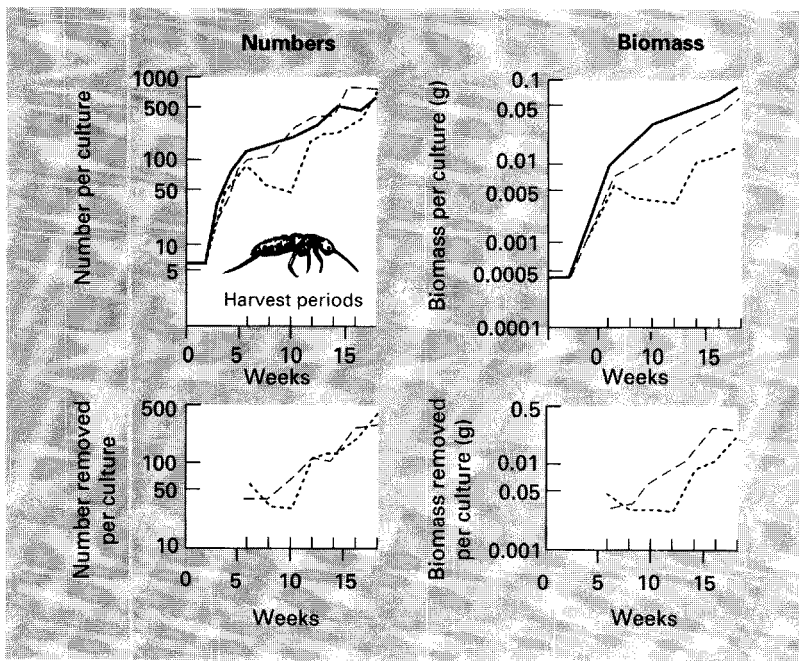


Fig. 5.55 The effects of exploitation on a population of the collembolan *Folsomia candida*; control, 0% exploitation (—); 30% exploitation (---); 60% exploitation (····). (After Usher *et al.*, 1971.)

taken with 30% exploitation yielded a higher biomass than with 60% exploitation, while the actual numbers of arthropods taken were approximately equal in the two regimes.

It is legitimate at this point to ask whether field populations of vertebrates behave in a similar way to these laboratory populations, and, regrettably, studying fish populations in the same detail presents almost intractable experimental problems. Silliman and Gutsell (1958), however, have succeeded in modelling the process of commercial fishing practices, with density-regulated populations of guppies (*Lebistes reticulatus*). Selective fishing, permitting small fish to escape, was applied every 3 weeks (corresponding to the reproductive periodicity of the fish), and the catch size was carefully controlled but changed after 40-week periods, so that the effects of a range of exploitation from 10 to 75% could be assessed. Although the results are by no means as clear as those we have examined so far, two points of interest are reinforced (Fig. 5.56). First, as we might expect, the size of the catch, measured as numbers or total biomass, was related to the level of exploitation: it was higher (though decreasing slightly) at 25% than it was at 10%, but at 50% it decreased

sharply, and at 75% it led to the extinction of the population. Thus, we have confirmation that the maximum sustainable biomass yield must be attained at some *intermediate* level of exploitation—probably close to or just below 25%. The second feature is that harvesting had a discernible effect on both the size-structure of the guppy population (since the mean length of the harvested fish declined noticeably with increasing exploitation), and the age-structure (Fig. 5.57). This, like the data on *Daphnia*, illustrates the general conclusion that the *structure of populations changes* when specific classes are exploited.

The guppy data also illustrate the process of overexploitation, i.e. of harvesting at a level in excess of the maximum which is sustainable. In contrast to the *Daphnia* data (see Fig. 5.54c), there appears to be a consistent *decline* in the proportion of the exploited, adult class between 25 and 75% exploitation (see Fig. 5.57). These higher exploitation-rates apparently result in a lowering of the adult proportion to a level that is unable to replenish the fish removed by harvesting. Increases in the fitness of survivors are insufficient to compensate for the decreases in numbers, and extinction would inevitably follow if harvest-

Fig. 5.56 Exploitation of guppy populations: biomass of the catch (—) number of fish caught (---), average length of harvested fish (.....). (After Silliman & Gutsell, 1958.)

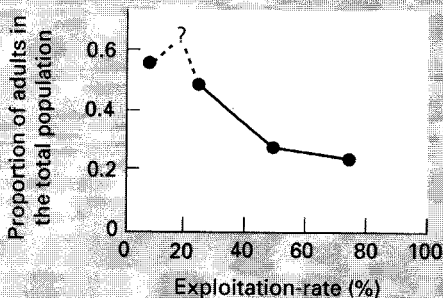
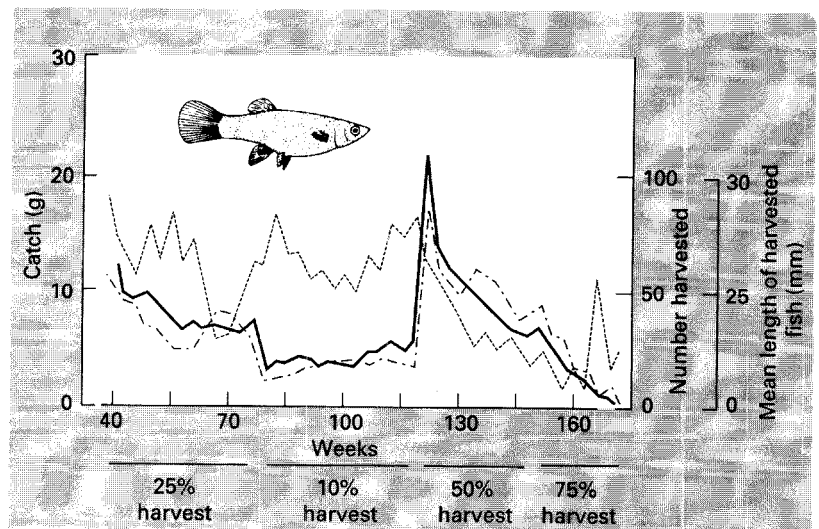


Fig. 5.57 Adult proportions in Silliman and Gutsell's (1958) guppy populations at different rates of exploitation, with the presumed relationship interpolated between the points.

ing at these levels (i.e. overexploitation) were to continue.

Comparisons between animals as different as *Daphnia* and guppies must obviously be carried out with caution. Nevertheless, it is interesting to note that when a very juvenile portion of the *Daphnia* populations is exploited, the maximum sustainable yield is obtained at a very high rate of exploitation (greater than 90%); but when adult guppies are exploited, the peak in sustainable yield occurs at a much lower exploitation-rate. It appears that in a structured population, higher exploitation-rates can be sustained if

juveniles are being exploited, because some of these juveniles would fail to reach maturity anyway. To generalize, we might suggest that maximal yields can be obtained from structured populations by removing those individuals that are likely to contribute least to the production of progeny in the future.

### 5.13.3 Incorporating population structure: matrix models of harvesting

In the logistic model of harvesting, we did not distinguish between age-classes of individuals; and this may justifiably be seen as a neglect of the significance of population structure and of age-specific fecundity and survival. Age-determined parameters can be incorporated into a model of a harvested population, however, by use of the matrix model from Chapter 3, and Usher (1972) has illustrated the practical application of this approach in an examination of the potential of the blue whale (*Balaenoptera musculus*) for harvesting. He collated data into a transition matrix describing the fecundity and survival of female blue whales, but as Table 5.10 shows, the paucity of these data necessitated the structuring of the population into only six 2-year age-classes up to the age of 12 and a single age-class thereafter (12+).

As explained in section 3.5, the subdiagonal elements of the matrix are measures of the probability of

**Table 5.10** Transition matrix for a population of female blue whales (After Usher, 1972.)

Age-class (years)	0-1	2-3	4-5	6-7	8-9	10-11	12+
0	0	0	0.19	0.44	0.5	0.5	0.45
0.77	0	0	0	0	0	0	0
0	0.77	0	0	0	0	0	0
0	0	0.77	0	0	0	0	0
0	0	0	0.77	0	0	0	0
0	0	0	0	0.77	0	0	0
0	0	0	0	0	0.77	0	0
0	0	0	0	0	0	0.77	0.78

survival from one class to the next (0.77 for each of the first six 2-year periods). Similarly, the lower right-hand corner element of the matrix is the 2-yearly survival-rate for females over 12. Its value of 0.78 gives individuals entering the 12+ class a mean life expectancy of 7.9 years; female blue whales can live to ages of between 30 and 40 years. The top row of values in the matrix give the fecundity terms for females: they reflect the fact that breeding does not start until the fifth year, and that full sexual maturity does not arrive until females are 7 years old. The fecundity terms of the 8-9 and 10-11 year classes are equal to 0.5, because females produce only one calf every 2 years and the sex ratio of the population is

1 : 1. The value for the 12+ class has been reduced to 0.45 to take account of irregular breeding in older whales.

Using the iterative procedure outlined previously (section 3.5), we can calculate the net reproductive rate of the population ( $R$ ) when it has achieved a stable age structure. This equals 1.0072, which, being very close to 1, indicates that the whale population can grow at only a very slow rate. We can now calculate the level of exploitation that the population can withstand, without entering a decline. In percentage terms this is  $\{(R - 1)/R\} \times 100$ , or 0.71%. In other words, the sustainable yield of the population every year is approximately 0.35% of every age-class. Harvesting-rates in excess of this would lead to losses that the species could not counteract unless homeostatic mechanisms acted to alter the fecundity and survival values in the matrix. In view of this, and the intensity with which whaling has been carried out, it is not surprising that blue whale numbers declined significantly in the early 1930s; and the species has been threatened ever since.

Further models, taking into account the effects of differentially exploiting different classes of a structured population, are beyond the scope of this book. The interested reader can consult Law (1979) and Beddington (1979).